ABSTRACT OF THESIS

PRESCRIBED FIRE EFFECTS ON OAK REGENERATION IN EASTERN KENTUCKY

In many oak-dominated forests in the eastern U.S. oak regeneration is poor and prescribed fire is assumed to benefit oak seedlings compared to fire sensitive species. However, the mechanisms and effectiveness remain poorly documented. We examined the effects of single and multiple fires on canopy structure and openness and seedling response. Hemispherical photography showed an increase of 3.8 % in canopy openness after burning, followed by a rapid reduction of 0.7 % per year after burning. The decrease in gap fraction coincided with the post-fire flush of the shrub stratum (> 50 cm in height and < 2 cm dbh, primarily tree sprouts), which approached the highest level (10,550 stems ha^{-1}) in 3 growing seasons after fire. We measured leaf mass per area (LMA, g m-2), leaf nitrogen content (N_{area}, $\mu g\ cm^{-2}$), photosynthetic response curve and maximum photosynthesis rate (A_{max}, $\mu mol\ CO_2\ m^{-2}\ s^{-1}$), stomatal conductance (g_{sw}, mol $H_2O\ m^{-2}\ s^{-1}$), height growth, total leaf area (TLA), and root collar diameter of chestnut oak (*Quercus prinus*), scarlet oak (*Q. coccinea*), and red maple (*Acer rubrum*) seedlings in the burned and control sites. Prescribed burning, with associated changes in gap fraction, significantly increased LMA, TLA, N_{area}, A_{max}, height growth, and total root mass; however, both oaks and red maple responded similarly to prescribed fire. The tendency of greater carbon allocation aboveground in red maple may increase its susceptibility to repetitive burning.

Key words: oak regeneration, prescribed fire, light, forest structure, *Quercus spp.*, *Acer rubrum*, hemispherical photography, photosynthesis

PRESCRIBED FIRE EFFECTS ON OAK REGENERATION IN EASTERN KENTUCKY

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The Graduate School

University of Kentucky

2002

PRESCRIBED FIRE EFFECTS ON OAK REGENERATION IN EASTERN KENTUCKY

THESIS

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Forestry at the University of Kentucky

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2002

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CHAPTER ONE

Quantifying the Effects of Prescribed Fire on Oak Understory Light Availability.

Introduction

Oak species (*Quercus spp.*) have dominated much of the central hardwood forest for at least 6,000 years (Watts 1979; Delcourt and Delcourt 1987; Delcourt et al. 1998). However, in the past several decades, declining success of oak vegetation has been attributed to a variety of possible causes, including poor seed production, acorn predation and consumption, damage to seedlings by animals, selective logging of oaks, disease, climate change, and excessive shade and competition (Abrams 1992, Lorimer 1993). Among the many factors that have been cited in causing poor oak regeneration, excessive shade from species with greater shade tolerance, such as red maple (*Acer rubrum* L.), is considered a key factor. This is corroborated by the fact that oaks are physiologically poorly adapted to a low light environment compared to their shade tolerant competitors (Abrams 1992; Lorimer 1993).

The dominance of oak species in North America has been closely related to recurring fire (Abrams 1992; Delcourt et al. 1998). Prehistoric Native Americans and post settlement Euro-Americans used fires for various purposes (Pyne 1982; Lorimer 1993; Delcourt and Delcourt 1998). Periodic fires caused mostly by those human activities were once an important force in arresting succession and maintain low stand density in the eastern deciduous forest (Abrams 1992). However, with continued fire suppression since the 1930s and 1940s, fires have been effectively prevented in much of the eastern deciduous forest and the beginning of widespread oak regeneration problems coincide remarkably well with the start of the federal fire suppression program (Lorimer 1993). Simultaneously, these forests were recovering from heavy logging and the aftermath of the chestnut blight (Keever 1953; McCormick and Platt 1980), both of which also have almost certainly contributed to the changing structure and composition.

Focusing on the apparent relationship between fire and poor oak regeneration, managers are increasingly using fire as a tool to regenerate oak species. However, little is known regarding the effectiveness of prescribed fire in the absence of forest thinning to alter stand structure and increase light availability to the seedling stratum. Although it can be argued that the understory light environment cannot be sufficiently altered without partial cutting, the effect of multiple prescribed fires on the light environment has not been specifically documented nor sufficiently examined. While preexisting studies suggest that a single fire does not alter stand structure, the effect of multiple prescribed fires on stand structure and light environment have rarely been documented (Robison and McCarthy 1999).

I investigated the effects of single and multiple prescribed fires on the understory light environment in upland oak forests on the Cumberland plateau in eastern Kentucky. The objectives of this study were to examine single and multiple prescribed fires to determine (1) the effects of prescribed fire on forest stand structure, (2) the interrelationships between prescribed fire, stand structure, and understory light environment, and (3) the persistence of changes in the understory light environment after burning.

Materials and Methods

Site Description

The study was conducted on Klaber (37°57'N, 83°37'W) and Whittleton ridges (37°46'N, 83°39'W) in the Red River Gorge Geological Area of Daniel Boone National

Forest of eastern Kentucky. This area is located in the Cliff Section of the Cumberland Plateau (Braun 1950). The sizes of the study areas, including burned and reference areas, were 30 to 40 ha. Annual precipitation at Heidelberg, in eastern Kentucky, is 1134 mm with the driest month in October (52 mm) and wettest in July (134 mm). Monthly mean temperature in January and July is 2.2°C and 24.2°C, respectively, with mean annual temperature 13.3°C (Hill 1976). The canopy species (>15 cm dbh) in the study areas are mostly composed of oak species (*Quercus coccinea* Muenchh., *Q. prinus* L., *Q. alba* L., *Q. velutina* Lam.) with some hard pines (*Pinus rigida* Mill., *P. virginiana* Mill., *P. echinata* Mill.) in the most xeric areas. The midstory (dbh between 2 and 15 cm) is mostly composed of blackgum (*Nyssa sylvatica* Marsh.), red maple, and sourwood (*Oxydendrum arboreum* [L.] DC.). The shrub stratum (> 50 cm in height and < 2cm dbh) is mostly composed of red maple, blackgum, eastern white pine (*P. strobus* L.), and sassafras (*Sassafras albidum* [Nutt.] Nees) (Arthur, unpublished data). Oaks are not important in either the midstory or shrub strata (less than 6% in relative density), although oak seedling density in the herbaceous stratum (stems <50 cm in height) was approximately 8000 seedlings/ha (Kuddes-Fischer and Arthur 2002).

Three prescribed fire treatment sites (2 burned and 1 reference) were established on each of Klaber and Whittleton ridges for long term monitoring of the effects of burning on oak regeneration and stand structure. Although originally designed in 1995 as a replicated experiment with two burn treatments and a reference on each of three ridges, weather-related constraints on prescribed burning reduced the design to burn treatments conducted in different years on two ridges. On Klaber Ridge, one site was burned three times, in the spring of 1995, 1999, and 2000; a second site was burned twice, in the spring of 1996 and 2000. On Whittleton Ridge, one site was burned twice in the spring of 1995 and 1999 and a second site was burned once in the spring of 1997. The different years of burning at four burned sites combined with two reference sites (one on each ridge) allowed us to test the effects of both fire frequency (number of burns) and the elapsed time since the last burn on stand structure and understory light environment. Prescribed fires were conducted by the USDA Forest Service personnel of the Stanton Ranger District. Table 1 summarizes the burn conditions in the four burned treatment sites in each burn year.

Field Sampling

Eight 0.05 ha permanent circular plots at each of the 6 sites were randomly established to measure the vegetation. I used data on the midstory (dbh 2-15 cm; collected from 1995 to 2001) and shrub (dbh < 2 cm, height > 50 cm; collected in 2000 and 2001) strata to characterize the effects of fire on stand structure.

Two 100 m transects were established at each of the 6 prescribed fire treatment sites in August 2000. At 20-meter intervals along each transect, the nearest seedling of each species, chestnut oak (*Q. prinus* L.), scarlet oak (*Q. coccinea Muenchh.*) and red maple, was marked for measurement of understory light (30 seedlings per site, 180 seedlings total). Hemispherical photographs were taken 60 cm above each seedling in the summer of year 2000 and 2001 to estimate gap fraction. For statistical analysis, I used the mean gap fraction of the 30 seedlings at each site, which was defined as an experimental unit. Stem density data collected in 2000 and 2001 were used in conjunction with measurements of understory light environment collected during the same period to characterize the effects of changes in the midstory stratum on understory

Table 1. Median fire temperature ranges (°C) and weather conditions of each prescribed fire event. Dashed lines indicate the years without burning.

Conditions	1995	1996	1997	1998	1999	2000
Klaber 3x burn (1995, 1999, 2000)						
Burn date	3/17	-	-	-	3/26	3/30
Temp. at 15 cm aboveground (°C)	316-398	-	-	-	400-499	500-659
Temp. at surface (°C)	316-398	-	-	-	198-249	250-399
Air temp. (°C)	21	-	-	-	8	9
Relative humidity (%)	36	-	-	-	40	35
Flame length (m)	0.3-0.9	-	-	-	0.3-0.9	0.3-0.9
Klaber 2x burn (1996, 2000)						
Burn date	-	3/13	-	-	-	3/30
Temp. at 15 cm aboveground (°C)	-	399-481	-	-	-	500-569
Temp. at surface (°C)	-	204-315	-	-	-	250-399
Air temp. (°C)	-	18	-	-	-	9
Relative humidity (%)	-	25	-	-	-	35
Flame length (m)	-	0.3-0.9	-	-	-	0.6-0.9
Whittleton 2x burn (1995, 1999)						
Burn date	3/15	-	-	-	3/26	-
Temp. at 15 cm aboveground (°C)	204-315	-	-	-	500-659	-
Temp. at surface (°C)	316-398	-	-	-	198-249	-
Air temp. (°C)	23	-	-	-	11	-
Relative humidity (%)	29	-	-	-	40	-
Flame length (m)	0.3-0.9	-	-	-	0.3-0.9	-

Table 1 (Continued).

Conditions	1995	1996	1997	1998	1999	2000
Whittleton 1x burn (1997)						
Burn date	-	-	3/24	-	-	-
Temp. at 15 cm aboveground (°C)	-	-	na	-	-	-
Temp. at surface (°C)	-	-	na	-	-	-
Air temp. (°C)	-	-	13	-	-	-
Relative humidity (%)	-	-	45	-	-	-
Flame length (m)	-	-	0.3-0.6	-	-	-

light. As I did not have gap fraction measurement at each permanent circular plots, the relationship between understory light environment and midstory stem density was characterized using 11 of the 24 permanent circular plots on Klaber Ridge for which I had gap fraction data available within 10 meters from the permanent circular plots. Although both measurements were not taken at the same location, light measurements using hemispherical photography within 20 meters were significantly spatially autocorrelated (Clark, et al. 1996).

Hemispherical photographs were taken using a Nikon Cool-Pix 950 digital camera with a Nikon FC-E8 183° fisheye converter. The photographs were taken during dusk and dawn, or on cloudy days, to prevent direct sunlight from entering the image. The digital images were first edited using Adobe Photoshop to eliminate noise and reflection, and then analyzed using GLA Version 2.0 canopy image analysis software (Frazer et al. 1999). The pixels within each image were classified into either sky or non-sky classes by assigning a threshold value, ranging from 0 to 255 (Frazer et al. 1999). Determination of the threshold value can cause biases in analyzing hemispherical photographs due to the incorporation of operator subjectivity (de Freitas and Enright 1995; Roxburgh and Kelly 1995). However, the operator biases can be insignificant with proper training before analysis (Robison and McCarthy 1999). To minimize the potential operator bias all photographs were analyzed by the same person and each photograph was analyzed repeatedly until two measurements of gap fraction were within 0.5% of each other (Canham et al 1990, Oberbauer et al. 1993). To avoid systematic error, the images were analyzed in random order. Other field protocols and details of hemispherical photography conformed to those described in Rich et al. (1999).

Data analysis

Because prescribed fires were conducted in different years in each site (Table 1), I divided the experimental units into two groups based on the similarities of treatments to form a 2 X 2 repeated-measures analysis of variance with 2 groups of prescribed burn treatments and 2 years of repeated measurements (von Ende 2001). The six sites were divided for analysis in two ways for the between-subjects (burn treatment) factors: (1) burned versus unburned and (2) multiple burned versus single burn and unburned. The within-subject factor was years of measurement (2000 and 2001), and allowed testing of change in the response variable over the one year period for which I had gap fraction data. Midstory stem density data prior to 2000 were not incorporated in the repeated-measures analysis because prescribed fire treatments were not completed until spring 2000 and using data prior to 2000 would result in an invalid grouping of between subject factors. All terms in repeated-measures ANOVA models were considered fixed effects and therefore were tested using the residual (error) mean square. Both repeated-measurements ANOVA and regression analysis were run with the GLM procedure in SAS (SAS institute 2000). P values less than 0.05 were considered to be statistically significant.

Results and Discussion

Effect of fire on midstory stem density

Prescribed burning had a significant effect on midstory stem density (stems 2-15 cm dbh; Table 2A, B). The effect was more significant when treatments were grouped into burned versus unburned ($p = 0.0061$; Table 2A), than for multiple versus single and unburned ($p=0.0357$; Table 2B). Midstory stem density at each burned site exhibited

Table 2. Analysis of variance of midstory stand density (stems 2-15cm dbh) with repeated measurements on treatment plots. Six treatment sites were divided for analysis in two ways: A: into burned vs. unburned (Grouping A) and B: into multiple burned vs. single and unburned (Grouping B). Two consecutive years of measurements were considered the main effect of within subject factors. The means of stand density at different sites and year were used for this analysis.

source of variation	df	mean square	F	P value
A. Grouping A (burned vs. unburned)				
Between subjects				
Treatment	1	1264315.51	27.99	0.0061
Error	4	45168.04		
Within subject				
Year	1	3015.04	1.87	0.2429
Year * Treatment	1	536.76	0.33	0.5945
Error (year)	4	1608.90		
B. Grouping B (multiple vs. single and unburned)				
Between subjects				
Treatment	1	1001890.78	9.04	0.0397
Error	4	110774.22		
Within subject				
Year	1	4413.13	2.89	0.1641
Year*Treatment	1	873.39	0.57	0.4913
Error (year)	4	1524.74		

substantial reduction after each prescribed fire (Figure 1). Thus, the differences in midstory stem density between pre-burn (1995) and 2001 were significantly correlated with the number of burns ($R^2 = 0.86$, $p = 0.0076$; Figure 2). On average, each burn reduced midstory stem density by approximately 550 stems per hectare. My findings agree with Peterson and Reich (2001), who showed a significant relationship between fire frequency and mean annual density change.

There was not a significant effect of the year of measurement (2000 and 2001) on stem density (Table 2A, B), revealing that between 2000 and 2001 there was no significant change in midstory stem density. Similarly, there was no clear trend (within 5 years after burning) of recovery in midstory stem density with increasing number of growing seasons after burning (Figure 3A). Thus, fire frequency did have a significant effect on stem density, and this effect was maintained in the midstory stratum for 3 to 5 years without significant ingrowth. Because oaks are not important in the midstory stratum in these sites (< 6 % in relative density), prescribed burning should have minimal impact on the advance of oak regeneration in the midstory while reducing the density of fire-sensitive species. This process also had great potential to increase light availability in the understory.

Effect of fire on canopy gap fraction

Prescribed burning had a significant effect on gap fraction, measured in the understory stratum using hemispherical photography. However, this effect was significant only when the sites were grouped into recent and multiple burns versus single and unburned ($p=0.0116$, Table 3B); it was not significant when sites were grouped into burned and unburned ($p=0.1195$, Table 3A).

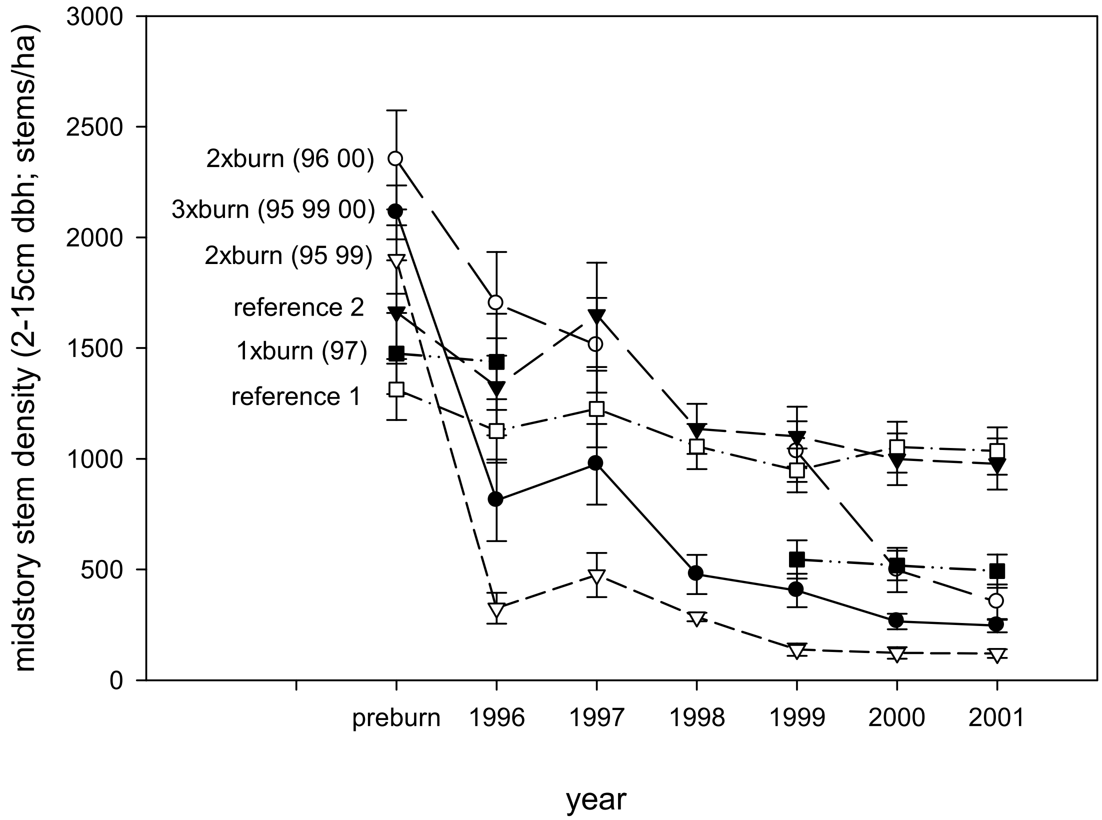

midstory stem density (2-15cm dbh; stems/ha)
3000
2500
2000
1500
1000
500
0
2xburn (96 00)
3xburn (95 99 00)
2xburn (95 99)
reference 2
1xburn (97)
reference 1
preburn
1996
1997
1998
1999
2000
2001
year

Figure 1

The dynamics of midstory stem density from 1995 to 2001.

The dynamics of midstory stem density (stems 2-15cm dbh) at different sites under different prescribed fire treatments. Numbers in parentheses are the years of burning. Error bars represent ± 1 SE.

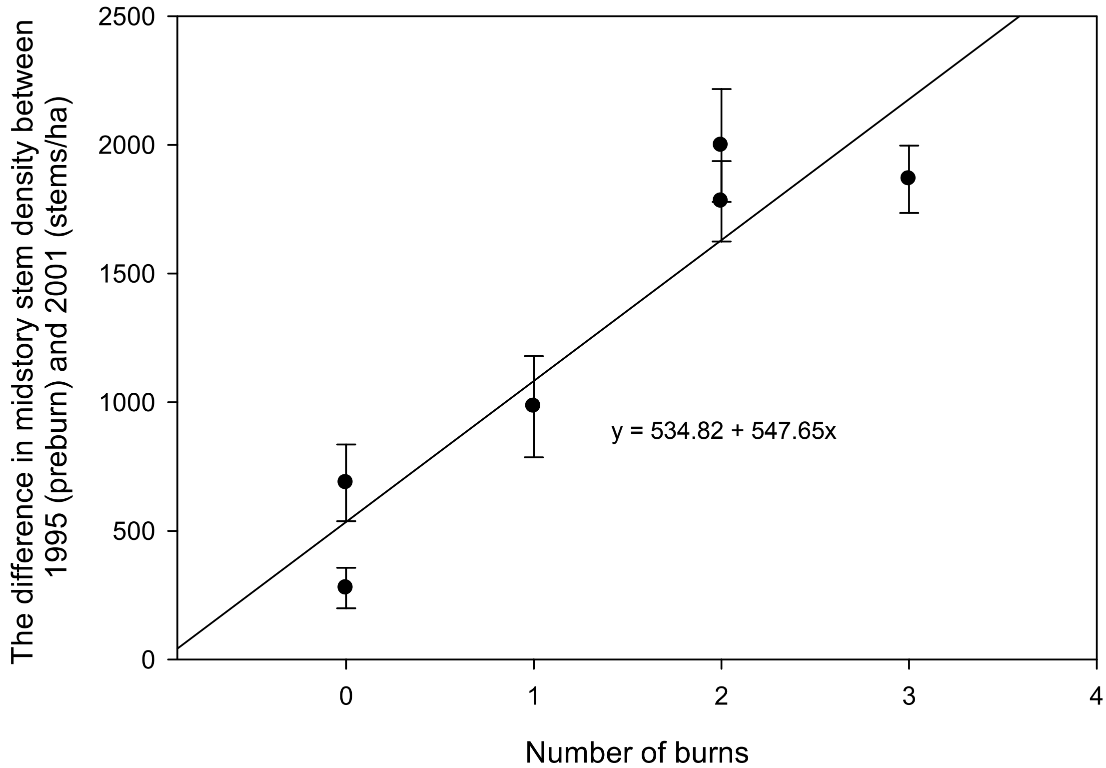
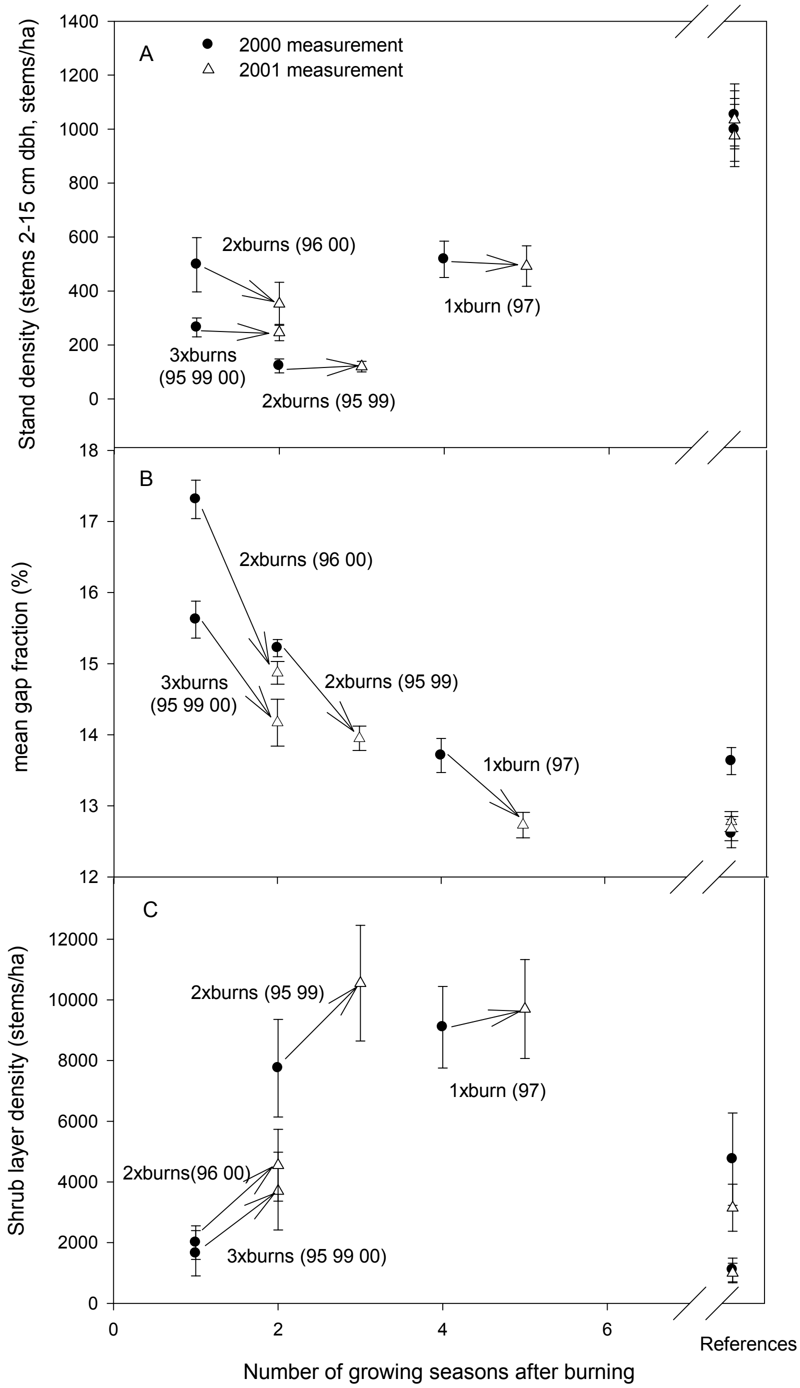

The difference in midstory stem density between 1995 (preburn) and 2001 (stems/ha)
0
500
1000
1500
2000
2500
y = 534.82 + 547.65x
0
1
2
3
4
Number of burns

Figure 2

The correlation between reduction in midstory stem density and number of burns.

The relationship between the mean differences of midstory stem density between preburn and 2001 post burn and the number of burns ($R^2 = 0.86$, $F_{1,4} = 16.03$, $p = 0.0076$). Error bars represent ± 1 SE.



A
2000 measurement
2001 measurement
Stand density (stems 2-15 cm dbh, stems/ha)
2xburns (96 00)
3xburns (95 99 00)
2xburns (95 99)
1xburn (97)
B
mean gap fraction (%)
2xburns (96 00)
3xburns (95 99 00)
2xburns (95 99)
1xburn (97)
C
Shrub layer density (stems/ha)
2xburns (95 99)
1xburn (97)
2xburns(96 00)
3xburns (95 99 00)
References
Number of growing seasons after burning

Figure 3

The post-fire changes in midstory and shrub layer density and gap fraction.

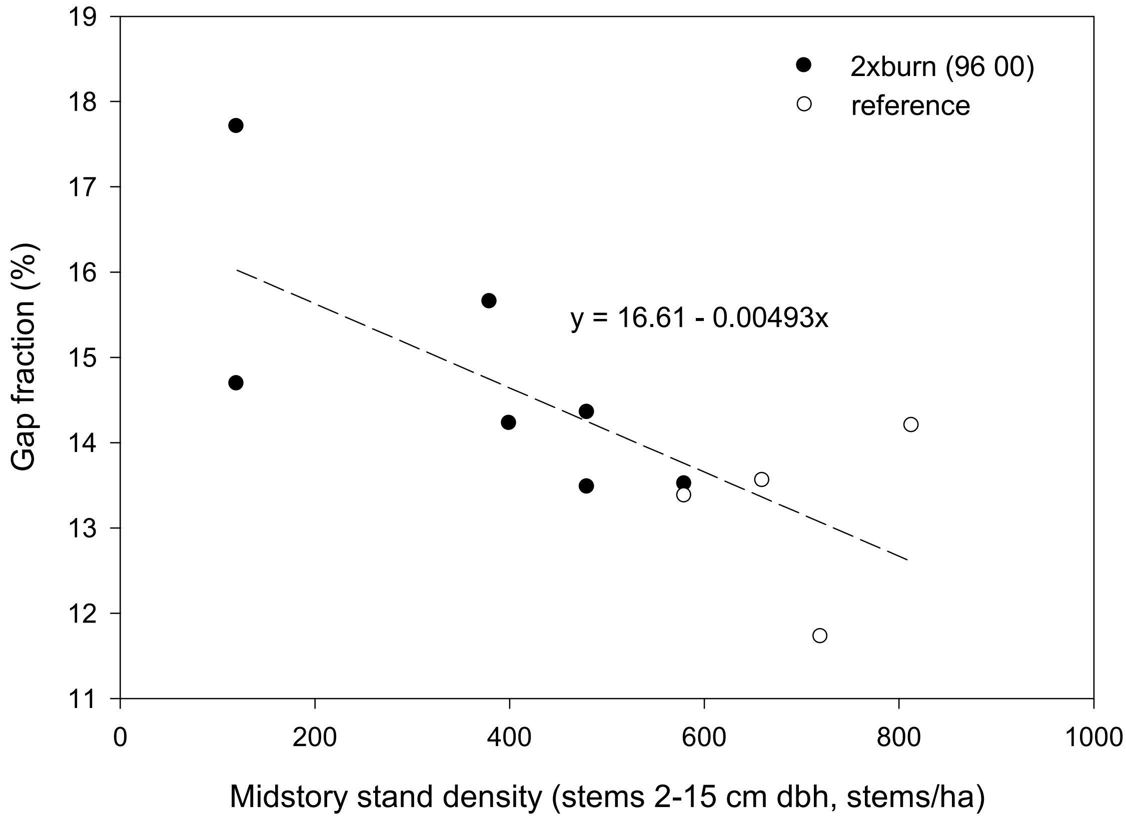
The temporal change of midstory stem density (stems 2-15 cm dbh, A), gap fraction (B), and shrub layer density (dbh < 2 cm, height > 50 cm, C) following burning. Error bars represent ± 1 SE.

Table 3. Analysis of variance of gap fraction with repeated measurements on treatment plots. Six treatment sites were divided for analysis in two ways: A: into burned vs. unburned (Grouping A) and B: into multiple burned vs. single and unburned (Grouping B). Two consecutive years of measurements were considered the main effect of within subject factors. The means of canopy openness at different sites and year were used for this analysis

source of variation	df	mean square	F	P value
A. Grouping A (burned vs. unburned)				
Between subjects				
Treatment	1	8.33	3.90	0.1195
Error	4	2.13		
Within subject				
Year	1	2.50	10.94	0.0297
Year * Treatment	1	0.88	3.90	0.1196
Error (year)	4	0.23		
B. Grouping B (multiple vs. single and unburned)				
Between subjects				
Treatment	1	14.00	19.45	0.0116
Error	4	0.72		
Within subject				
Year	1	4.04	19.78	0.0113
Year*Treatment	1	0.99	4.83	0.0928
Error (year)	4	0.20		

For a subset of sites (Klaber Burn 1996 & 2000, Klaber reference) I had measurements of gap fraction for individual vegetation plots, which enabled us to examine the relationship between midstory stem density and gap fraction. There was a significant relationship between gap fraction and midstory stand density ($p = 0.01$, $R^2 = 0.56$, Figure 4) measured in 2001, indicating the important control of midstory stem density over the understory light environment. However, while the post-fire midstory stem density did not exhibit any trend of recovery (Figure 3A), I found a rapid and continuous decrease in gap fraction from 16.46% to 12.73 % in five growing seasons after fire (Figure 3B). The time elapsed since the last burn was highly significantly related to the gap fraction measured in the understory ($p = 0.0040$, $R^2 = 0.77$, Figure 3B).

Thus as expected, midstory stem density was not the only factor that impacted the understory light environment. The decrease in gap fraction after burning (Figure 3B) coincided with the increase in shrub density (18%- 75% sprout in the reference sites, 44%-100% sprout in the burned sites) after burning (Figure 3C). The flush of growth in the shrub stratum after burning undoubtedly played an important role in the short-term dynamics of the understory light environment after burning. While burning reduced midstory stand density, resulting in a temporary increase in gap fraction, a strong sprouting response increased stem density in the shrub stratum, resulting in a decrease in gap fraction. Although gap fraction and midstory stem density were negatively and significantly correlated (Figure 4), this relationship was based on the data from two sites only, Klaber 2x burn (96, 00) and Klaber reference (Figure 4), where shrub layer density was relatively low (Figure 3C). Thus, the short-term (one year) change in gap fraction was well explained by the short-term change in shrub density. The rapid increase in



2xburn (96 00)
reference
y = 16.61 - 0.00493x
Gap fraction (%)
Midstory stand density (stems 2-15 cm dbh, stems/ha)
19
18
17
16
15
14
13
12
11
0
200
400
600
800
1000

Figure 4

The correlation between gap fraction and midstory stem density.

The relationship between midstory stand structure and canopy openness (R^2 = 0.52, $F_{1,9}$ = 10.08, p = 0.01). All data were measured in Klaber ridge.

shrub density after burning approached the highest level (10,550 stems/ha) in three growing seasons after fire. Thus, the shrub layer can be more important than canopy layer in hindering oak regeneration (Lorimer et al. 1994).

In examining the effect of the number of growing seasons since the last burn, I used each site as a space for time substitution of years since burning. This approach assumes homogeneous conditions among sites with respect to the parameters I measured and the treatment regimes (fire prescription). Unfortunately, pre-burn midstory density exhibited significant pre-burn site variation ($p = 0.0016$; Figure 1), and, although lacking pre-burn data for gap fraction and shrub layer density, these parameters also exhibited variation among reference sites (Figure 3B and 3C). However, with repeated measurements in 2000 and 2001, the data exhibited a consistent decrease in gap fraction and a coincident increase in shrub layer density (Figure 3B and 3C) while the reference sites had relatively minor variation between two years of measurements. The midstory density, on the other hand, did not exhibit significant differences between repeated measurements of 2000 and 2001 (Figure 3A).

Although the canopy trees intercept most of the light, the midstory co-dominant and understory shrub strata also have important impacts on the understory light environment, and both strata are subject to the impact of prescribed burning. Post fire midstory density remained stable for 3 to 5 years; in contrast, the shrub layer density increased about 5 fold in 3 growing seasons after burning. The fast flush of sprouts in the shrub layer mitigated the influence on the understory light environment of the midstory canopy gaps created by prescribed fire. The increased light environment in the Klaber 2x burn (96, 00) site due to prescribed fire was significantly correlated with leaf mass per area of chestnut oak, scarlet oak and red maple seedlings, which subsequently influenced the leaf nitrogen content and photosynthetic capacity (Chiang and Arthur in preparation). However, those relationships were similar among the three species, indicating that all species responded similarly.

The relatively high midstory stem density and low shrub layer density (Figure 3A and 3C) in the reference sites indicated the effects of the absence of fire on forest stand structure. Soon after prescribed fire, the shrub-layer (primarily composed of tree sprouts) increased markedly in stem density. Many of these stems will grow into the mid-story resulting, perhaps, in increased mid-story density in the references relative to the burned sites (Fig 3A). In the absence of fire, this increased mid-story density, coupled with the growth of surviving mid-story stems creates low light conditions in the understory. Ultimately, then, suppressing survivorship in the shrub-layer such that densities return to a relatively low level.

Different fire regimes (e.g. fire intensity, frequency, time elapsed after last burn) for each site can be a source of error in my analysis. Although there were different prescribed fire frequencies and burning regimes among different sites (Table 1), the last fire event on each site, which was more crucial for my space-for-time analysis of shrub layer density and gap fraction, had similar burning intensity and weather conditions (Table 1). The number of growing seasons post fire is probably more important in affecting gap fraction and shrub layer density than the number of burns. On the other hand, midstory stem density did not exhibit a trend of recovery after fire treatment within the timeframe of my study, and the effects of burning on the midstory density accumulate with additional fire events. As a result, the differences in midstory stem density between

1995 pre-burn and 2001 were significantly correlated with the number of burns ($p = 0.0076$, $R^2 = 0.86$; Figure 2). Although the number of burns and the time elapsed since the last burn are confounded, I assume the later has a small impact on the midstory stem density.

In summary, my data suggest that prescribed burning can significantly reduce the midstory stem density, thereby temporarily increasing light in the understory. However, the understory shrub layer (mostly sprouts), which increased rapidly in density after fire, mitigated the influence of canopy gaps created by prescribed fire. Managers whose goal is to improve oak regeneration by increasing the understory light environment through the use of prescribed burning will need to control the flush of the shrub layer in order to maintain the effectiveness of fire in creating more light in the understory. These results suggest that prescribed fires, with intervals of longer than every 3-5 years or in the absence of other control measures, will be unlikely to create the necessary light environment for successful oak regeneration.

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CHAPTER TWO

Single and Multiple Prescribed Fire Effects on Seedling Performance in an Upland Oak Forest

Introduction

Oak species (*Quercus spp.*) have dominated much of the eastern deciduous forest for at least 6,000 years (Watts 1979; Delcourt and Delcourt 1987; Delcourt et al. 1998). The dominance of oak species in North America has been closely related to recurring fire (Abrams 1992; Delcourt et al. 1998), used by prehistoric Native Americans and post settlement Euro-Americans for various purposes (Pyne 1982; Lorimer 1993; Delcourt and Delcourt 1998). Periodic fires caused mostly by those human activities were once an important force that kept forests in early succession and maintained low stand density in the eastern deciduous forest (Abrams 1992). However, deliberate fire suppression since the 1930s has contributed toward increased stand density and a reduction in understory light, which are considered key factors in causing poor oak regeneration. Oaks are physiologically poorly adapted to a low light environment compared to their shade tolerant competitors (Abrams 1992; Lorimer 1993), leading to understory and midstory composition increasingly dominated by more mesic species. Simultaneously, these forests have been recovering from heavy logging and the aftermath of the chestnut blight (Keever 1953; McCormick and Platt 1980).

Among the oak competitors, red maple (*Acer rubrum* L.) has been considered the most aggressive species that dominates in the midstory and thrives in the shrub and herb strata in my study area (Arthur et al. 1998), and throughout much of the region (Lorimer 1984, Abrams 1998). Although the overstory is dominated by oak species and oak seedling density in the herbaceous stratum (stems <50 cm in height) is moderately high (approximately 8000 seedlings/ha; Kuddes-Fischer and Arthur 2002), there is a lack of oak regeneration in the shrub (>50 cm height, < 2cm dbh) and midstory (2-10 cm dbh) strata. This bimodal distribution of oak abundance with respect to size class clearly demonstrates the long-term problems in oak regeneration.

Increasingly, managers are trying to address the lack of successful oak regeneration by reintroducing fire to the landscape, with the hope that fire will restore the processes that can facilitate oak regeneration. However, there is still controversy regarding the effectiveness of prescribed fire on oak regeneration, especially the use of single fire, which may promote robust resproutings by oak competitors (Lorimer 1993, Arthur et al. 1998, Kuddes-Fischer and Arthur 2002). Although multiple fires have the potential to promote oak success by reducing the viability of resprouting red maple, the effectiveness of this strategy has so far been undocumented.

The objectives of this study were to investigate the morphological and physiological responses of chestnut oak (*Q. prinus* L.), scarlet oak (*Q. Coccinea* Muench.), and red maple seedlings to single and multiple fires to improve our understanding of the effects of increased light availability following fire prescription on seedling performance. I hypothesized that the three species would have significant physiological and morphological responses to prescribed fire and the associated changes in light environment, and that the effects would be more pronounced in the sites burned multiple times. Moreover, I also hypothesized that prescribed fire, and the consequent changes in understory light environment, would have differential effects on the seedling performance of the three species, with oaks favored more than red maple by increasing number of burns.

Materials and Methods

Site description and prescribed fire

The study was conducted on Klaber (37°57'N, 83°37'W) and Whittleton ridges (37°46'N, 83°39'W) in the Red River Gorge Geological Area of Daniel Boone National Forest of eastern Kentucky. This area is located in the Cliff Section of the Cumberland Plateau (Braun 1950). Annual precipitation at Heidelberg, in eastern Kentucky, is 1134 mm with the driest month in October (52 mm) and wettest in July (134 mm). Monthly mean temperature in January and July is 2.2°C and 24.2°C, respectively, with mean annual temperature 13.3°C (Hill 1976). The soils in Klaber ridge are classified as Latham silt loam and Latham-Shelocta silt loam which belong to the clayey, mixed, mesic Aquic Hapludults family and are slowly permeable, moderately deep, and moderately well drained, formed in material weathered from shale and siltstone (Avers et al. 1974). The soils in Whittleton ridge are composed of Gilpin silt loam and Gilpin-Shelocta complex belonging to fine-loamy, mixed, mesic typic Hapludults family. They are moderately deep and well drained, formed in loamy material weathered from siltstone, sandstone, and shale (Hayes, 1993). The canopy trees (> 15 cm dbh) in the study areas are mostly composed of oak species (*Quercus coccinea* Muenchh., *Q. prinus* L., *Q. alba* L., *Q. velutina* Lam.) with some hard pines (*Pinus rigida* Mill., *P. virginiana* Mill., *P. echinata* Mill.) in the most xeric areas. The midstory (dbh between 2 and 15 cm) is mostly composed of red maple, blackgum (*Nyssa sylvatica* Marsh.), and sourwood (*Oxydendrum arboreum* [L.] DC.) The shrub stratum (> 50 cm in height and < 2cm dbh,) is mostly composed of red maple, blackgum, eastern white pine (*P. strobus* L.), and sassafras (*Sassafras albidum* [Nutt.] Nees). Oaks are not important in either the midstory or shrub strata (less than 6% in relative density), although oak seedling density in the herbaceous stratum (stems <50 cm in height) is approximately 8000 seedlings/ha (Kuddes-Fischer and Arthur 2002).

Three prescribed fire treatments (2 burned and 1 reference) were established on each of Klaber and Whittleton ridges for long term monitoring of the effects of burning on oak regeneration and stand structure. Although originally designed in 1995 as a replicated experiment with each of two burn treatments and a reference on each of three ridges, problems with conducting burns reduced the design to burn treatments conducted in different years on two ridges. On Klaber Ridge, one site was burned three times, in the spring of 1995, 1999, and 2000; the other site was burned twice, in the spring of 1996 and 2000. On Whittleton Ridge, one site was burned twice in the spring of 1995 and 1999 and the other site was burned once in the spring of 1997. Prescribed fires were conducted by the USDA Forest Service personnel of the Stanton Ranger District. Table 1 summarizes the burn conditions in the four burned treatment sites in each burn year.

Field sampling and lab analysis

Two 100 m transects were established on each of the 6 prescribed fire treatment sites in August 2000. At 20-meter intervals along each transect, the nearest seedling of each species, chestnut oak, scarlet oak, and red maple, was sampled (30 seedlings per site, 180 seedlings total).

Hemispherical photographs were taken 60 cm above each seedling using a Nikon Cool-Pix 950 digital camera with a Nikon FC-E8 183° fisheye converter. More details on the acquisition and analysis of hemispherical photographs can be seen in Chapter 1.

Table 1. Median fire temperature ranges (°C) and weather conditions of each prescribed fire event. Dashed lines indicate the years without burning.

Conditions	1995	1996	1997	1998	1999	2000
Klaber 3x burn (1995, 1999, 2000)						
Burn date	3/17	-	-	-	3/26	3/30
Temp. at 15 cm aboveground (°C)	316-398	-	-	-	400-499	500-659
Temp. at surface (°C)	316-398	-	-	-	198-249	250-399
Air temp. (°C)	21	-	-	-	8	9
Relative humidity (%)	36	-	-	-	40	35
Flame length (m)	0.3-0.9	-	-	-	0.3-0.9	0.3-0.9
Klaber 2x burn (1996, 2000)						
Burn date	-	3/13	-	-	-	3/30
Temp. at 15 cm aboveground (°C)	-	399-481	-	-	-	500-569
Temp. at surface (°C)	-	204-315	-	-	-	250-399
Air temp. (°C)	-	18	-	-	-	9
Relative humidity (%)	-	25	-	-	-	35
Flame length (m)	-	0.3-0.9	-	-	-	0.6-0.9
Whittleton 2x burn (1995, 1999)						
Burn date	3/15	-	-	-	3/26	-
Temp. at 15 cm aboveground (°C)	204-315	-	-	-	500-659	-
Temp. at surface (°C)	316-398	-	-	-	198-249	-
Air temp. (°C)	23	-	-	-	11	-
Relative humidity (%)	29	-	-	-	40	-
Flame length (m)	0.3-0.9	-	-	-	0.3-0.9	-

Table 1 (Continued).

Conditions	1995	1996	1997	1998	1999	2000
Whittleton 1x burn (1997)						
Burn date	-	-	3/24	-	-	-
Temp. at 15 cm aboveground (°C)	-	-	na	-	-	-
Temp. at surface (°C)	-	-	na	-	-	-
Air temp. (°C)	-	-	13	-	-	-
Relative humidity (%)	-	-	45	-	-	-
Flame length (m)	-	-	0.3-0.6	-	-	-

I used a LI-3000A portable area meter (Li-Cor Inc., Lincoln, NE, U.S.A.) to measure total leaf area (TLA, cm^2) of each seedling. A 16mm diameter leaf disk was sampled from each seedling and oven-dried for 72 hours at 60 °C to obtain dry mass and estimate leaf mass per area (LMA, g m^{-2}). The oven-dried leaf disks were analyzed for Nitrogen concentration (N_{mass}, LECO CN2000). Leaf nitrogen content per area (N_{area}) was calculated by multiplying N_{mass} by LMA. Seedling annual height growth (mm) was measured between the scars left by terminal bud scales of two consecutive winters under the assumption of a single flush per year. Relative height growth was calculated using the following equation from Hunt (1990):

[1] $(\ln HT_{fin} - \ln HT_{ini}) / t$

Where HT_{fin} and HT_{ini} were the final and initial seedling height measurements. HT_{ini} was estimated by subtracting the last year's height growth from HT_{fin}. The time, t, was 1 year.

All seedlings, including both shoot and root, were excavated at the end of growing season in late November 2000. The seedlings were first removed from the ground by digging up 70-cm diameter by 40-cm depth cylinders of soil with shovels and shaken by hand in the field until the soils detached from the root to ensure the least loss of fine roots. The whole seedlings were kept below 0°C until processed. Within 24 hours, seedlings were processed as follows. Seedlings were first washed with tap water to remove remaining soil and then washed with de-ionized water. Roots and shoots were separated by cutting at the root collar. The upper 50 mm sections of roots were flash frozen with liquid N and ground with mortar and pestle and stored at -20°C for later root starch analysis. Roots were analyzed for starch following Quarmby and Allen (1989).

To elucidate the effects of prescribed fire on seedling photosynthesis, in August 2001, two growing seasons after the most recent burning in the spring of 2000, I selected 15 seedlings of each of chestnut oak, scarlet oak, and red maple in Klaber (96, 00) and Klaber reference sites (45 seedlings per site, 90 seedlings total). The seedlings were selected to cover the full range of gap fraction found within each site based on the previous year's gap fraction data. Photosynthetic light response curves and stomatal conductance to water vapor (g_{sw}) of each of the 90 seedlings were measured from August 8 to August 16 between the hours of 0900 and 1400 using a Li-Cor LI-6400 portable photosynthesis system (Li-Cor Inc., Lincoln, NE, U.S.A.) equipped with a standard leaf chamber, Li-Cor LED red and blue light source (LI-6400-02), and external CO2 source assembly (LI-6400-01). Leaf cuvett temperature (26 ± 4°C) and relative humidity (65 ± 5 %) were kept at ambient level. Measurements were made on fully expanded leaves and acclimated to a level of photosynthetically active radiation (PAR) at 1500 µmol m^{-2} s^{-1} for the first measurement. The subsequent measurements were made by decreasing the PAR level to 1000, 500, 200, 100, 50, 10, and 0 µmol m^{-2} s^{-1}. CO_2 concentration in the sample analyzer was kept constant at 350 µmol mol^{-1}. Data were not logged until the total coefficient of variation, which includes the coefficients of variation of differential CO_2 and H_2O concentration between the sample and reference analyzers and flow rate, was less than 1%. I also measured gap fraction, height growth, TLA, LMA, N_{mass}, and N_{area} of seedlings sampled in 2001.

Data analysis

Each seedling was treated as an experimental unit; therefore, species differences were analyzed in a completely randomized design. However, because the prescribed burning treatments were not replicated, using the seedling as the experimental unit to detect fire treatment effects results in pseudoreplication at the site and treatment levels (Hurbert 1984). Thus, I cannot separate the fire treatment effects from other inherent differences between the sites. In the 2000 study (180 seedlings) I analyzed the fire treatment effects separately for the two ridges to eliminate the effects of differences between two ridges. Thus, the treatment and species effects were examined separately with one-way analysis of variance (ANOVA) using general linear model (PROC GLM) in SAS (SAS institute 2000). Statistical significance between means was determined using least square differences (LSD) test. Analysis of covariance (ANCOVA, PROC GLM) was used to examine both categorical and continuous variables. In addition, we performed two sample t-tests (PROC TTEST in SAS; SAS institute 2000) to evaluate the divergence of population means at each burned site from its nearby reference site. The t-value, which is the ratio of the difference in means between two sites and the standard error of differences between two means, provided a standardized measure of divergence of means. Fire treatment effects on seedling responses can be revealed by the coordination between the divergence of means between the burned and its nearby reference sites and the frequency and recency of burning. The denominator of the t-value was estimated differently depending on the equality of sample variance and Satterthwaite's method for computing degrees of freedom were used when sample variances were significantly different (Snedecor and Cochran 1989).

A light response curve for each of the 90 seedlings in the 2001 study was fitted with the Michaelis-Menten model (Givnish 1988; Kloeppel et al. 1993) using a non-linear model in SAS (PROC NLIN; SAS institute 2000):

[1] $A = (A_{max\text{-}area}/PAR)/ (PAR + K) - Rs$

where

A is net photosynthesis (μmol m^{-2} s^{-1})

$A_{max\text{-}area}$ is maximum photosynthesis on area basis (μmol m^{-2} s^{-1})

PAR is photosynthesis active radiation (μmol m^{-2} s^{-1})

K is saturation constant, which is the level of PAR to achieve one half of $A_{max\text{-}area}$

Rs is dark respiration (μmol m^{-2} s^{-1})

The light compensation point was calculated by obtaining PAR of the fitted model with A = 0.

Relationships between continuous variables were examined with simple linear regression using general linear model (PROC GLM) in SAS (SAS institute 2000). P values less than 0.05 were considered to be statistically significant.

Results

Seedling growth and carbon allocation in response to prescribed fire

Gap fraction was significantly greater in the burned than in the reference sites except for the Whittleton (97) site, which was burned four growing seasons before data collection and had similar gap fraction to the Whittleton reference site (Table 2). Interestingly, this site also was burned with the lowest intensity (Table 1). Due to an increase in shrub density following fire, the effect of prescribed burning on gap fraction

Table 2. Growth and leaf characteristics of chestnut oak, scarlet oak, and red maple seedlings under different prescribed fire treatments (n = 10). Numbers in parenthesis indicate years of burn. All parameters were measured in the summer of 2000 except total root mass and % root starch which were measured and excavated in November 2000. Data from the two ridges were analyzed separately. Different upper case letters indicate significant differences among sites within row. Different lower case letters indicate significant differences among species within each site. Statistical significance between means was determined using least square differences (LSD) test with $p<0.05$. Value t indicates the deviation of mean at the burned sites with regard to the control site in units of standard error. Relative height growth for seedlings at both burned sites in Klaber ridge were not presented because there was no initial heigh after burning in the spring of 2000.

Variable	species	Klaber (95 99 00)			Klaber (96 00)			Klaber control	
		mean	se	t	mean	se	t	mean	se
Gap fraction (%)	Chestnut oak	15.27	0.45 Ba	3.72	17.06	0.42 Aa	6.65	12.67	0.41 Ca
	Scarlet oak	16.22	0.41 Ba	7.47	17.43	0.51 Aa	8.40	12.52	0.28 Ca
	Red maple	15.38	0.50 Ba	4.48	17.44	0.51 Aa	7.73	12.63	0.36 Ca
Height growth (mm)	Chestnut oak	94.70	9.41 Ab	5.06	112.30	11.88 Aa	5.43	25.70	7.05 Ba
	Scarlet oak	111.10	8.05 Aab	10.15	119.50	10.26 Aa	9.01	21.40	3.65 Bab
	Red maple	135.50	11.25 Aa	10.93	149.10	23.70 Aa	5.78	11.90	1.13 Bb
Relative height growth	Chestnut oak	-			-			0.41	0.24 a
	Scarlet oak	-			-			0.14	0.03 a
	Red maple	-			-			0.07	0.01 a
Total root mass (g)	Chestnut oak	1.93	0.32 ABb	2.57	2.32	0.53 Ab	2.33	1.09	0.09 Bb
	Scarlet oak	4.52	0.26 ABa	0.79	8.01	2.13 Aa	1.99	3.16	1.18 Ba
	Red maple	3.31	0.58 Aab	3.41	3.19	0.91 Ab	2.15	1.18	0.23 Bab
% root starch (%)	Chestnut oak	5.17	0.33 Aa	-0.27	2.95	0.26 Ba	-3.85	5.13	0.51 Aa
	Scarlet oak	2.84	0.17 Ab	1.36	2.42	0.10 Ab	-0.49	2.52	0.17 Ab
	Red maple	2.13	0.18 Bc	-2.04	2.58	0.13 ABab	-0.61	2.75	0.25 Ab

Table 2(Continued).

Variable	species	Klaber (95 99 00)			Klaber (96 00)			Klaber control	
		mean	se	t	mean	se	t	mean	se
Total root starch (g)	Chestnut oak	0.10	0.02 Aa	2.46	0.07	0.02 ABb	0.93	0.05	0.01 Ba
	Scarlet oak	0.13	0.04 Aa	0.68	0.19	0.05 Aa	1.57	0.09	0.04 Aa
	Red maple	0.07	0.01 ABa	2.44	0.08	0.03 Ab	2.00	0.03	0.01 Ba
TLA (cm^2)	Chestnut oak	86.19	13.22 Ab	-0.27	114.90	14.86 Ab	1.13	102.86	15.46 Aa
	Scarlet oak	173.61	27.09 ABa	1.65	215.40	34.07 Aa	2.50	123.72	13.61 Ba
	Red maple	126.73	13.30 Aab	4.18	126.45	22.05 Ab	2.73	62.67	7.62 Bb
LMA ($g\ m^{-2}$)	Chestnut oak	49.71	2.17 Aa	3.06	51.56	2.39 Aa	3.47	40.23	1.33 Bb
	Scarlet oak	51.34	1.54 ABa	1.92	51.76	1.62 Aa	2.06	47.25	1.48 Ba
	Red maple	41.64	2.03 Bb	1.27	46.99	0.95 Aa	5.91	38.76	1.02 Bb
N_{mass} (%)	Chestnut oak	1.60	0.06 Ba	-0.23	1.85	0.09 Aa	1.96	1.59	0.06 Ba
	Scarlet oak	1.73	0.06 Ba	4.70	2.16	0.21 Aa	3.63	1.39	0.04 Bb
	Red maple	1.58	0.10 Ba	4.30	2.12	0.23 Aa	4.30	1.13	0.03 Cc
N_{area} ($\mu g\ cm^{-2}$)	Chestnut oak	79.44	4.47 Ba	2.43	94.77	4.73 Aa	5.45	63.86	2.41 Ca
	Scarlet oak	88.85	3.63 Ba	5.96	112.18	12.05 Aa	3.85	65.51	1.48 Ca
	Red maple	64.64	2.96 Bb	6.51	99.77	11.33 Aa	4.92	43.72	1.24 Cb

Table 2(Continued).

Variable	species	Whittleton (95 99)			Whittleton (97)			Whittleton control	
		mean	se	t	mean	se	t	mean	se
Gap fraction (%)	Chestnut oak	15.31	0.20 Aa	4.38	13.73	0.37 Ba	0.23	13.62	0.33 Ba
	Scarlet oak	15.12	0.19 Aa	3.46	13.53	0.41 Ba	-0.18	13.63	0.39 Ba
	Red maple	15.21	0.23 Aa	4.22	13.87	0.51 Ba	0.38	13.64	0.29 Ba
Height growth (mm)	Chestnut oak	30.90	1.86 Ab	4.92	35.60	4.67 Aa	3.63	16.90	2.16 Bb
	Scarlet oak	43.70	5.93 Aab	2.59	39.80	4.22 Aa	2.53	25.80	3.58 Ba
	Red maple	61.70	9.02 Aa	4.75	34.80	7.77 Ba	2.13	17.50	2.29 Bb
Relative height growth	Chestnut oak	0.24	0.03 Aa	4.99	0.20	0.02 Aa	5.79	0.09	0.01 Ba
	Scarlet oak	0.28	0.05 Aa	2.69	0.19	0.01 ABa	1.88	0.13	0.03 Ba
	Red maple	0.32	0.04 Aa	5.47	0.20	0.05 Ba	1.71	0.11	0.01 Ba
Total root mass (g)	Chestnut oak	3.49	0.83 Ab	1.83	4.30	1.53 Aab	1.56	1.84	0.35 Ab
	Scarlet oak	7.39	0.42 Aa	0.67	8.09	1.84 Aa	0.87	5.86	1.79 Aa
	Red maple	2.74	0.21 Ab	0.66	2.99	0.55 Ab	0.81	1.97	1.14 Ab
% root starch (%)	Chestnut oak	3.50	0.22 Aa	-0.13	3.52	0.52 Aa	-0.05	3.55	0.30 Aa
	Scarlet oak	2.27	0.08 ABb	-1.01	1.88	0.08 Bb	-2.61	2.52	0.23 Ab
	Red maple	2.04	0.08 Ab	-1.49	2.13	0.11 Ab	-1.02	2.36	0.20 Ab
Total root starch (g)	Chestnut oak	0.12	0.03 Aab	1.79	0.15	0.07 Aa	1.22	0.06	0.01 Ab
	Scarlet oak	0.17	0.03 Aa	0.81	0.16	0.04 Aa	0.46	0.13	0.04 Aa
	Red maple	0.06	0.01 Ab	2.45	0.06	0.01 Aa	2.30	0.03	0.01 Bb

Table 2(Continued).

Variable	species	Whittleton (95 99)			Whittleton (97)			Whittleton control	
		mean	se	t	mean	se	t	mean	se
TLA (cm^2)	Chestnut oak	147.00	21.38 Ab	0.51	181.97	32.13 Ab	1.28	130.79	23.93 Ab
	Scarlet oak	299.14	33.01 Aa	1.84	326.49	50.98 Aa	1.88	209.31	35.91 Aa
	Red maple	190.28	21.26 Ab	3.92	123.10	12.51 Bb	1.79	87.99	15.16 Bb
LMA ($g\ m^{-2}$)	Chestnut oak	49.04	1.49 Aab	4.09	43.84	1.15 Bb	1.47	41.52	1.08 Bb
	Scarlet oak	54.64	2.28 Aa	3.40	47.98	1.09 Ba	1.30	45.89	1.19 Ba
	Red maple	48.06	2.02 Ab	4.42	41.65	1.74 Bb	1.88	37.71	1.18 Bc
N_{mass} (%)	Chestnut oak	1.47	0.05 Bb	-3.82	1.77	0.08 Aa	0.72	1.71	0.04 Aa
	Scarlet oak	1.68	0.04 Ba	0.93	1.84	0.06 Aa	3.73	1.64	0.02 Ba
	Red maple	1.36	0.05 ABb	1.86	1.46	0.08 Ab	2.45	1.24	0.04 Bb
N_{area} ($\mu g\ cm^{-2}$)	Chestnut oak	72.66	4.34 Ab	0.46	77.86	4.56 Ab	1.55	70.57	1.20 Aa
	Scarlet oak	92.06	5.23 Aa	2.94	90.93	3.69 Aa	3.51	75.39	2.63 Ba
	Red maple	65.22	3.43 Ab	4.47	60.20	2.91 Ac	3.69	46.27	2.31 Bb

diminished with increasing antecedent period (Chiang et al., in preparation). The t-value of gap fraction, which is a measure of deviation from the mean in a burned site compared to its reference, also decreased with increasing antecedent period, the duration of the non-fire period between the last prescribed fire and 2000 (year of measurement, Table 2).

Seedling height growth of all species was significantly greater in the burned compared to the reference site except red maple in the Whittleton (97) site (Table 2). Like gap fraction, the effects tended to diminish (decreasing t value) with longer duration of the antecedent period; therefore, the prescribed burning effect on seedling height growth was more pronounced on Klaber ridge where seedlings in both burned sites resprouted from topkilled seedlings after prescribed burning in the spring of 2000. Red maple tended to have greater height growth than the oaks in the sites burned multiple times (both burned sites in Klaber ridge and the multiple burned site in Whittleton ridge), while oaks tended to have slightly greater height growth than red maple in the Whittleton (97) and reference sites. Relative height growth followed a similar pattern to that of height growth on Whittleton Ridge. Relative height growth for both burned sites on Klaber Ridge were unavailable because all seedlings had no initial height in 2000 due to topkilling by the prescribed fire.

Belowground carbon allocation was influenced by burn treatment. Total root mass was greater in the burned than in the reference sites on Klaber ridge but was similar among sites on Whittleton ridge (Table 2). Scarlet oak had significantly greater root mass than the other two species in all sites. Root starch concentrations tended to be lower in the burned than reference sites; however, there was no systematic pattern of t values regarding antecedent period and fire frequency, suggesting that neither factor affects root starch concentration (Table 2). There was a tendency for total root starch, the product of total root mass and root starch concentration, to be greater in the burned sites than the reference on both ridges, and greater in oaks than in red maple, although most comparisons were not significant and primarily reflect differences in total root mass. Despite relatively low total root mass, chestnut oak had significantly greater root starch concentration than the other two species.

I hypothesized that gap fraction, regardless of burn treatment, would be correlated with carbon allocation patterns. The relationships between height growth and gap fraction were significant for all three species with all sites combined ($0.34 < R^2 < 0.55$; $p < 0.0001$). However, when analyzed by site and species separately, only scarlet oak on Klaber (96, 00) site ($R^2 = 0.44$, $p = 0.0379$) and red maple on Whittleton (97) site ($R^2 = 0.40$, $p = 0.0461$) were significant. Thus, the significant correlations between height growth across sites for respective species were mainly contributed by the tendency of greater height growth on the most recently burned sites (with greater gap fraction) and lower height growth on the reference sites (with lower gap fraction) but not by more subtle differences in gap fraction within site. This is evidenced by the analysis of covariance model in which gap fraction became insignificant ($p \geq 0.2088$) with the addition of the site effect ($p < 0.0001$), and suggests that other factors in addition to light contribute importantly to height growth. The relationships between gap fraction and total root mass were not significant for any species analyzed either across or within sites. The sample size (10 seedlings per species per site) and gap fraction range (less than 6%) may not be large enough to detect the relationship between gap fraction and carbon allocation.

In 2001, 15 seedlings of each of chestnut oak, scarlet oak, and red maple on Klaber (96, 00) and Klaber reference sites (90 seedlings total) were selected based on the previous year's gap fraction measurements to reflect the broadest range of light availability expressed on my study sites. I did not excavate those seedlings to estimate root mass because they are part of a long term seedling population study. Instead, I used the relationship between root collar diameter and root mass developed for the seedlings which were excavated in November 2000 to estimate root biomass in the intact seedlings (Table 3). The relationships were all significant and R^2 were between 0.68 and 0.96.

Seedlings that were measured in 2001 on Klaber ridge had similar patterns in height growth to those measured in 2000 (Table 4). Both height growth and relative height growth of seedlings of all three species were significantly greater on the Klaber (96, 00) site, two growing seasons after burning, than the reference site (Table 4). Note that differences, while significantly higher on the Klaber (96, 00) site, were much lower than in 2000. The observation of greater height growth of burned site sprouts compared to unburned has been observed previously (Kruger and Reich 1997) and attributed to increased allocation of carbon to height growth versus secondary growth in response to topkilling by fire. Further, indeterminate growth of first year sprouts, even among oaks, can lead to greater growth the first year after fire followed by much slower growth in subsequent year. Consistent with the 2000 data, chestnut oak had the greatest, while red maple had the lowest, height growth in the Klaber reference site, whereas red maple had the greatest height growth on the Klaber (96, 00) site and the largest difference between Klaber (96, 00) and Klaber reference sites ($t = 3.09$; Table 4). Relative height growth among the three species were not significantly different in the reference site, whereas, red

Table 3. Coefficients of regression equations for total root dry mass (g) as a linear function of root collar diameter (cm): total root mass = a * root collar diameter. Linear regression model were built with the assumption of no interception.

Site	species	a	se	R2	p-value
Klaber (96 00)	Chestnut oak	0.387	0.052	0.86	<0.0001
	Scarlet oak	0.869	0.199	0.68	0.0018
	Red maple	0.564	0.156	0.62	0.0068
Klaber control	Chestnut oak	0.228	0.015	0.96	<0.0001
	Scarlet oak	0.665	0.097	0.84	<0.0001
	Red maple	0.358	0.056	0.82	<0.0001

Table 4. Seedling growth, leaf and photosynthetic characteristics of chestnut oak, scarlet oak, and red maple seedlings in burned and control sites. Data were measured in the summer of 2001. Different letters indicate significant differences between species within each site. Statistical significance between means was determined using least square differences test with $p<0.05$. Two samples t-test was used to determine the differences between burned and control. P-value identicates significant level of differences between burned and control site at each row.

		Klaber (96, 00)				Klaber Control					
Variables	species	n	mean	se		n	mean	se		t	P-value
Gap fraction (%)	Chestnut oak	14	15.04	0.46	a	15	13.24	0.36	a	3.12	0.0042
	Scarlet oak	14	14.38	0.27	a	15	13.32	0.37	a	2.26	0.0320
	Red maple	14	14.86	0.40	a	13	12.81	0.32	a	3.97	0.0065
Height growth (mm)	Chestnut oak	14	44.79	4.31	ab	15	27.20	7.50	a	2.03	0.0047
	Scarlet oak	14	33.29	6.63	b	15	17.73	2.93	ab	2.15	0.0458
	Red maple	14	75.36	20.77	a	13	11.08	1.60	b	3.09	0.0086
Relative height growth	Chestnut oak	14	0.39	0.03	ab	15	0.16	0.03	a	9.40	<0.0001
	Scarlet oak	14	0.33	0.06	b	15	0.12	0.02	ab	6.53	<0.0001
	Red maple	14	0.54	0.09	a	13	0.06	0.01	b	4.71	<0.0001
Estimated root mass (g)	Chestnut oak	14	1.13	0.05	c	15	0.62	0.03	c	8.56	<0.0001
	Scarlet oak	14	2.38	0.18	a	15	1.87	0.12	a	2.37	0.0249
	Red maple	14	1.66	0.18	b	13	1.24	0.10	b	2.03	0.0563
TLA (cm2)	Chestnut oak	14	102.92	10.36	a	15	111.73	16.66	a	-0.44	0.6624
	Scarlet oak	14	131.32	17.46	a	15	105.40	13.89	a	1.17	0.2523
	Red maple	14	141.27	37.99	a	13	104.17	17.78	a	0.88	0.3878
LMA (g/m2)	Chestnut oak	14	50.48	2.03	b	15	40.99	1.61	b	3.69	0.0010
	Scarlet oak	14	58.68	2.34	a	15	47.30	1.13	a	4.38	0.0003
	Red maple	14	45.80	1.54	b	13	38.56	1.02	b	3.86	0.0007

Table 4(Continued).

		Klaber (96, 00)				Klaber Control					
Variables	species	n	mean	se		n	mean	se		t	P-value
N_{mass} (%)	Chestnut oak	14	1.79	0.07	a	15	1.84	0.07	a	-0.54	0.5966
	Scarlet oak	14	1.68	0.06	ab	15	1.80	0.04	a	-1.75	0.0914
	Red maple	14	1.57	0.06	b	13	1.57	0.06	b	0.01	0.9946
N_{area} (µg/cm2)	Chestnut oak	14	90.48	5.65	a	15	74.85	3.32	b	2.42	0.0223
	Scarlet oak	14	98.64	5.32	a	15	84.86	1.82	a	2.45	0.0262
	Red maple	14	71.99	3.82	b	13	60.04	1.86	c	2.81	0.0113
$A_{max\text{-}area}$ (µmol CO_2 m^{-2} s^{-1})	Chestnut oak	14	6.02	0.57	b	15	4.10	0.36	b	2.89	0.0076
	Scarlet oak	14	7.84	0.59	a	15	5.97	0.21	a	3.00	0.0084
	Red maple	14	5.16	0.38	b	13	3.89	0.26	b	2.73	0.0114
$A_{max\text{-}mass}$ (nmol CO_2 g^{-1} s^{-1})	Chestnut oak	14	119.89	9.76	a	15	103.01	9.40	b	1.25	0.2235
	Scarlet oak	14	135.68	10.66	a	15	126.96	4.99	a	0.74	0.4680
	Red maple	14	112.03	6.54	a	13	102.15	7.60	b	0.99	0.3321
K (µmol photon m^{-2} s^{-1})	Chestnut oak	14	57.91	9.19	ab	15	38.63	3.35	b	1.97	0.0660
	Scarlet oak	14	71.39	7.71	a	15	46.92	2.12	a	3.06	0.0079
	Red maple	14	46.42	4.44	b	13	32.51	2.15	b	2.82	0.0110
Rs (µmol CO_2 m^{-2} s^{-1})	Chestnut oak	14	0.50	0.09	a	15	0.28	0.05	a	2.20	0.0369
	Scarlet oak	14	0.50	0.09	a	15	0.33	0.06	a	1.71	0.0994
	Red maple	14	0.35	0.04	a	13	0.20	0.04	a	2.70	0.0122
LCP (µmol photon m^{-2} s^{-1})	Chestnut oak	14	5.21	0.99	a	15	3.11	0.57	a	1.87	0.0728
	Scarlet oak	14	5.05	1.04	a	15	2.79	0.44	a	2.01	0.0601
	Red maple	14	3.44	0.53	a	13	1.77	0.36	a	2.56	0.0169

maple had significantly greater relative height growth than oaks on Klaber (96, 00) site (Table 4). Estimated root mass of all species was significantly greater on the Klaber (96, 00) site than the Klaber reference site (Table 4). In both sites, scarlet oak had the greatest, and chestnut oak the lowest, root mass, also consistent with the 2000 data.

Because gap fraction and total leaf area (TLA) are important in plant carbon acquisition, I examined the correlation between height growth and root mass with gap fraction and TLA for each species individually. For relationships that were significant or marginally significant ($p < 0.1$), red maple had greater slopes for the relationships between height growth and both gap fraction and TLA, although the differences in slopes among species were not significant (Table 5; Figure 1). Conversely, scarlet oak had greater slopes for the relationships between root mass and both gap fraction and TLA. The tests of slope differences among species were significant in the root mass: gap fraction relationship in the burned site and root mass: TLA relationship in the reference site (Table 5).

Leaf characteristics

Oaks had similar TLA in the burned compared to the reference sites (measured in 2000) except for scarlet oak at Klaber (96, 00) site, where TLA was significantly greater than on the Klaber reference site (Table 2). Red maple, on the other hand, had consistently greater TLA in the multiple burned than on the reference sites (Table 2). Leaf mass per area (LMA) showed clear fire treatment effects on both ridges and was significantly greater on multiple and more recently burned sites than either the reference or Whittleton (97) sites. The exceptions to this were for scarlet oak and red maple on the

Table 5. Summary of linear regression analysis (Y = a + bX) . Different letters indicate significant differences of intercepts (a) and slopes (b) between species for each site. Pooled models were presented when species had no significant effect on a and

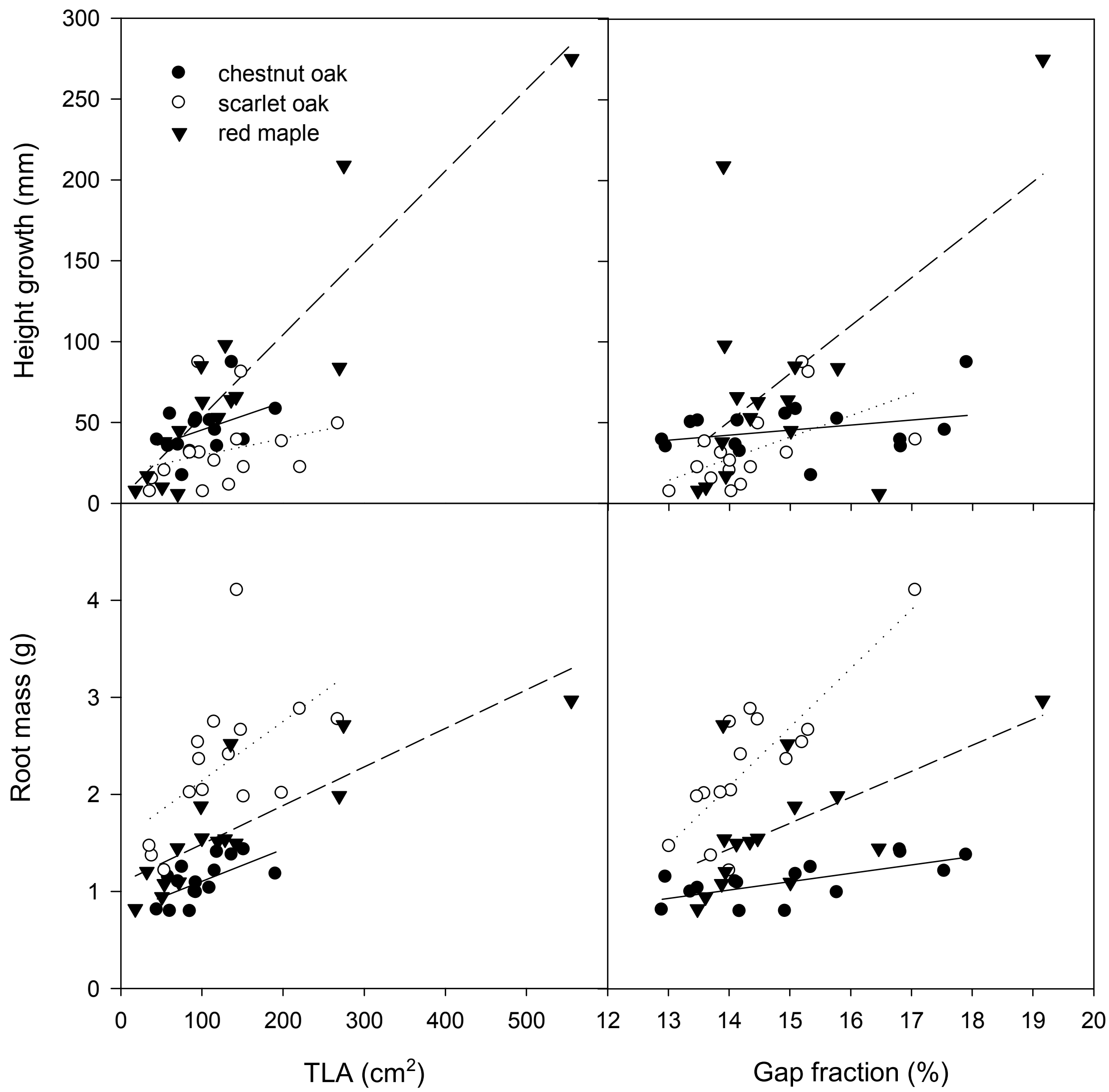
Y	X	site	species	a	b	R^2	F	p-value
Height growth	gap fraction	Klaber	Chestnut oak	-2.357 a	3.136 b	0.11	1.49	0.2453
		(96, 00)	Scarlet oak	-155.914 ab	13.157 ab	0.29	4.89	0.0471
			Red maple	-369.999 b	29.977 a	0.34	6.11	0.0294
		Klaber	Chestnut oak	77.509 a	-3.800 a	0.03	0.44	0.5198
		Control	Scarlet oak	50.975 a	-2.495 a	0.10	1.47	0.2476
			Red maple	53.732 a	-3.331 a	0.43	8.46	0.0142
			pooled	51.722	-2.489	0.03	1.21	0.2769
Root mass	gap fraction	Klaber	Chestnut oak	-0.153 a	0.085 b	0.54	13.91	0.0029
		(96, 00)	Scarlet oak	-5.987 b	0.582 a	0.75	36.51	<0.0001
			Red maple	-2.319 ab	0.268 b	0.36	6.71	0.0236
		Klaber	Chestnut oak	0.887 ab	-0.020 b	0.07	1.05	0.3251
		Control	Scarlet oak	3.465 a	-0.120 b	0.14	2.19	0.1626
			Red maple	-1.163 b	0.188 a	0.35	5.91	0.0333
Total leaf area	gap fraction	Klaber	Chestnut oak	-100.797 b	13.549 b	0.36	6.68	0.0239
		(96, 00)	Scarlet oak	-53.030 b	12.820 b	0.04	0.50	0.4951
			Red maple	-939.482 a	72.747 a	0.59	17.55	0.0013
		Klaber	Chestnut oak	385.482 a	-20.680 a	0.20	3.15	0.0991
		Control	Scarlet oak	406.056 a	-22.568 a	0.37	7.60	0.0163
			Red maple	-54.138 a	12.362 a	0.05	0.56	0.4712
			pooled	286.700	-13.661	0.09	4.18	0.0475

Table 5(Continued).

Y	X	site	species	a	b	R^2	F	p-value
Height growth	TLA	Klaber	Chestnut oak	23.509 a	0.207 ab	0.25	3.93	0.0707
		(96, 00)	Scarlet oak	20.432 a	0.098 b	0.07	0.85	0.3734
			Red maple	3.892 a	0.506 a	0.86	71.33	<0.0001
		Klaber	Chestnut oak	-1.920 a	0.261 a	0.34	6.56	0.0237
		Control	Scarlet oak	5.005 a	0.121 ab	0.33	6.33	0.0258
			Red maple	11.828 a	-0.007 b	0.01	0.07	0.7940
Root mass	TLA	Klaber	Chestnut oak	0.828 a	0.003 a	0.32	5.68	0.0346
		(96, 00)	Scarlet oak	1.697 a	0.005 a	0.25	3.96	0.0698
			Red maple	1.101 a	0.004 a	0.70	28.30	0.0002
			pooled	1.142	0.005	0.32	18.75	<0.0001
		Klaber	Chestnut oak	0.506 b	0.001 b	0.41	9.07	0.0100
		Control	Scarlet oak	1.152 a	0.007 a	0.65	23.89	0.0003
			Red maple	0.916 a	0.003 b	0.31	4.97	0.0476
LMA	gap fraction	Klaber	Chestnut oak	10.701 a	2.646 a	0.36	6.65	0.0242
		(96, 00)	Scarlet oak	-19.814 a	5.459 a	0.40	7.97	0.0154
			Red maple	15.594 a	2.033 a	0.28	4.72	0.0507
			pooled	19.398	2.186	0.12	5.42	0.0251
		Klaber	Chestnut oak	54.643 a	-1.032 a	0.05	0.71	0.4139
		Control	Scarlet oak	62.707 a	-1.157 a	0.15	2.23	0.1592
			Red maple	47.690 a	-0.713 a	0.05	0.70	0.4668
			pooled	50.389	-0.604	0.02	0.72	0.4010

Table 5(Continued).

Y	X	site	species	a	b	R^2	F	p-value
N_{area}	LMA	Klaber	Chestnut oak	-14.509 a	2.080 a	0.56	15.10	0.0022
		(96, 00)	Scarlet oak	6.624 a	1.568 a	0.48	10.91	0.0063
			Red maple	-10.095 a	1.792 a	0.52	13.13	0.0035
			pooled	-8.243	1.844	0.61	62.13	<0.0001
		Klaber	Chestnut oak	25.486 a	1.204 a	0.34	6.73	0.0223
		Control	Scarlet oak	37.688 a	0.997 a	0.39	8.15	0.0135
			Red maple	47.297 a	0.331 a	0.03	0.37	0.5560
			pooled	6.887	1.578	0.49	39.76	<0.0001
N_{area}	N_{mass}	Klaber	Chestnut oak	-21.895 a	62.925 a	0.60	18.57	0.0010
		(96, 00)	Scarlet oak	-6.574 a	62.537 a	0.47	10.58	0.0069
			Red maple	-7.705 a	50.816 a	0.61	18.44	0.0010
			pooled	-18.860	63.077	0.52	43.38	<0.0001
		Klaber	Chestnut oak	20.241 a	29.724 a	0.35	6.88	0.0211
		Control	Scarlet oak	57.600 a	15.137 a	0.09	1.33	0.2698
			Red maple	22.477 a	22.686 a	0.49	10.33	0.0081
			pooled	8.737	37.364	0.41	27.94	<0.0001
$A_{max\text{-}area}$	N_{area}	Klaber	Chestnut oak	0.954 a	0.056 a	0.31	5.40	0.0385
		(96, 00)	Scarlet oak	1.496 a	0.064 a	0.34	6.15	0.0290
			Red maple	1.406 a	0.052 a	0.28	4.69	0.0512
			pooled	0.461	0.068	0.43	30.18	<0.0001
		Klaber	Chestnut oak	0.137 a	0.053 a	0.24	4.00	0.0668
		Control	Scarlet oak	3.301 a	0.031 a	0.08	1.06	0.3215
			Red maple	-0.835 a	0.079 a	0.31	5.02	0.0466
			pooled	-0.322	0.068	0.42	30.09	<0.0001



chestnut oak
scarlet oak
red maple
Height growth (mm)
Root mass (g)
TLA (cm^2)
Gap fraction (%)

Figure 1

The carbon allocation patterns of chestnut oak, scarlet oak and red maple.

Relationships among seedling growth (height growth and root mass) and both total leaf area (TLA) and gap fraction for chestnut oak, scarlet oak, and red maple seedlings in Klaber (96, 00) site.

Klaber (95, 99, 00) site, where LMA was similar to the Klaber reference site. Scarlet oak had significantly greater TLA than the other two species except on the Klaber reference site where the oak species had similar TLA. Scarlet oak also had greater LMA than red maple (Table 2).

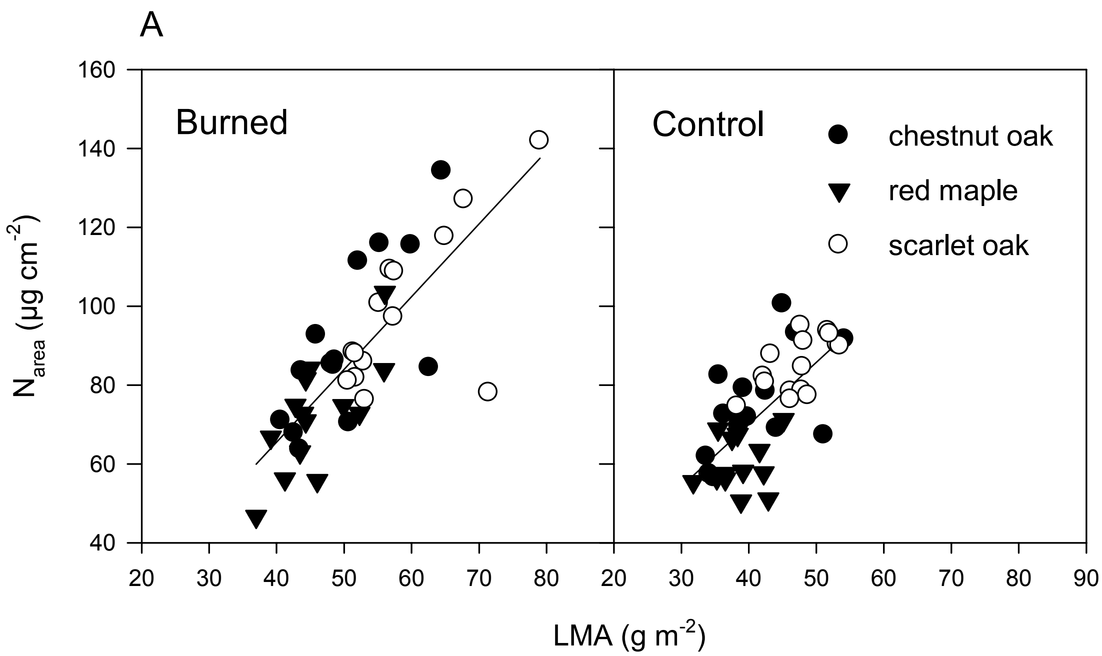
Leaf nitrogen per mass (N_{mass}) did not exhibit systematic responses to either antecedent period or frequency of fire. Chestnut oak had either similar or lower foliar N_{mass} in burned compared to reference sites. Scarlet oak and red maple had greater N_{mass} in both Klaber burned sites and Whittleton (97) site than the reference sites ($t \geq 2.45$, $p < 0.03$). However, N_{mass} of both species was similar in the Whittleton (95, 99) and Whittleton reference site (Table 2). This may indicate the presence of other environmental effects of the respective sites on N_{mass} other than fire treatments. Among species, oaks tended to have greater N_{mass} than red maple, although the species effect was not significant in either burned site on Klaber ridge. N_{area}, which was the product of LMA and N_{mass}, was greater in the burned sites than in the reference on both ridges (except chestnut oak on Whittleton ridge, which had similar values on burned and reference sites). N_{area} tended to be greater in oaks than in red maple (Table 2).

Seedlings that were sampled in 2001, two years after burning, had similar results in leaf characteristics to those sampled in 2000; however, the differences of TLA, N_{mass} and N_{area} between burned and reference sites were either more moderate or insignificant (Table 4). LMA on both Klaber (96, 00) and Klaber reference sites exhibited no significant changes between 2000 and 2001 measurements. Like measurements in 2000, oaks generally had greater LMA and N_{mass} leading to significantly greater N_{area} of oaks than red maple (Table 4; Fig. 2B and 2C). The site differences of N_{area} in the 2001 measurements were mainly contributed by the significant differences of LMA between the two sites because N_{mass} was similar (Table 4; Figure 2B). The similar N_{mass} between the two sites for 2001 measurements may reflect a transient increase in soil nitrogen availability after burning (Prieto-Fernandez et al. 1993).

I hypothesized that leaf characteristics would be correlated with gap fraction. Seedlings that were sampled in 2001 had greater sample size per species per site and therefore were used to examine the relationships between leaf characteristics and gap fraction. LMA of all species and TLA of chestnut oak and red maple on the the Klaber (96, 00) site were significantly correlated with gap fraction (Table 6). N_{area} was significantly correlated with LMA ($R^2 > 0.49$, $p < 0.0001$; Figure 2A; Table 5). Thus, on Klaber (96, 00) site, the increase in LMA with increasing gap fraction had the potential to elevate N_{area}, which is significantly correlated with $A_{max\text{-}area}$ (Table 5). However, only chestnut oak exhibited a significant relationship between gap fraction and N_{area} on the Klaber (96, 00) site (Table 6) and this is due to the erratic relationship between gap fraction and N_{mass}. The relationships on the Klaber reference site were either not significant or significant but in the reverse direction (Table 6).

Light response curves and photosynthetic characteristics

A light response curve was fitted for each seedling in the 2001 study using the Michaelis-Menten model (Givnish 1988). Model R^2, calculated as the ratio of model sum of squares to total sum of squares for each of the 85 seedlings (5 seedlings were not measured due to the loss of foliage) was greater than 0.99. The means of $A_{max\text{-}area}$, K, and Rs (Table 4) were used in the Michaelis-Menten model to produce six light response


A
Burned
Control
chestnut oak
red maple
scarlet oak
N_{area} (µg cm^{-2})
LMA (g m^{-2})
160
140
120
100
80
60
40
20
30
40
50
60
70
80
90

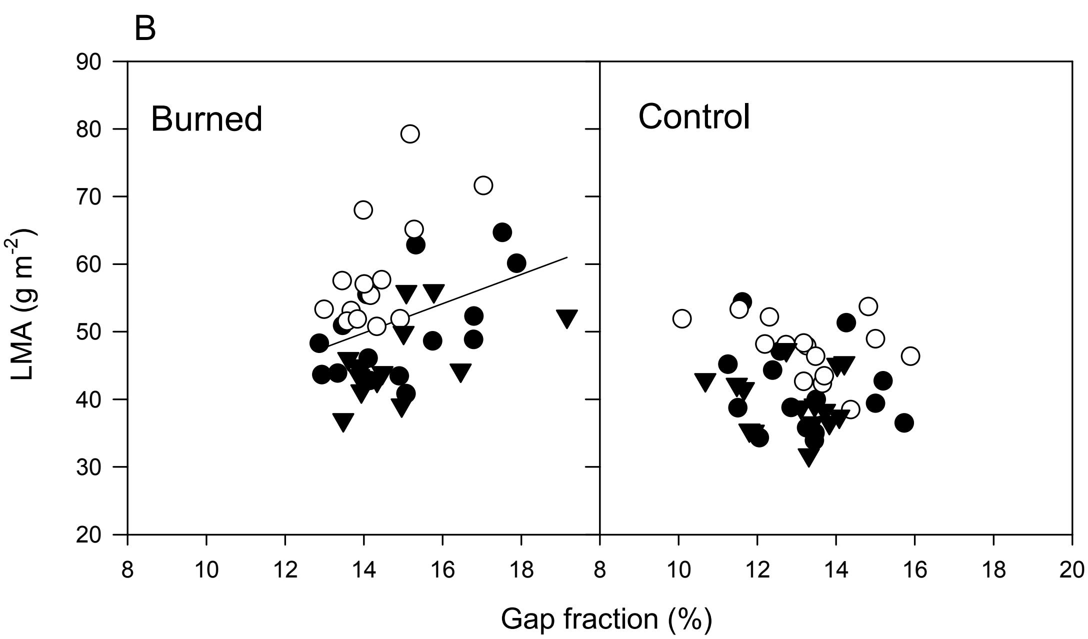

B
Burned
Control
LMA (g m^{-2})
Gap fraction (%)
90
80
70
60
50
40
30
20
8
10
12
14
16
18
20

Figure 2

The correlations among leaf nitrogen content, leaf mass per area, and gap fraction.

Relationships among leaf nitrogen content per area basis (N_{area}), specific leaf mass (SLM), and gap fraction. Data were pooled for chestnut oak, scarlet oak, and red maple because relationships were not significantly different among species. Regression statistics were given in Table 5.

Table 6. Pearson correlation coefficients of the relationships between gap fraction and both leaf and photosynthetic characteristics. Data were measured in the summer of 2001, two growing seasons after burning.

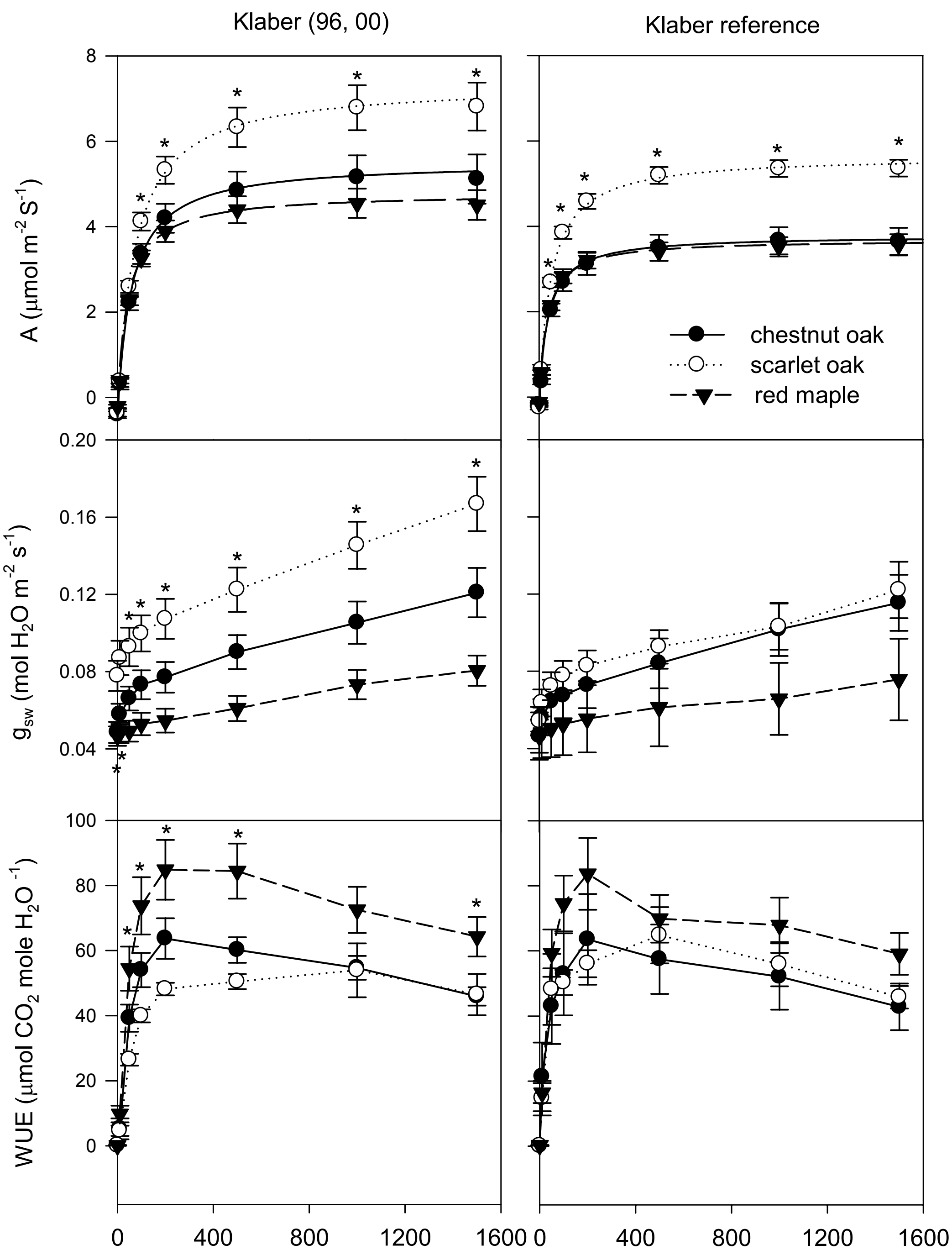
	Klaber (96, 00)			Klaber reference		
	Chestnut oak	Scarlet oak	Red maple	Chestnut oak	Scarlet oak	Red maple
Leaf characteristics						
TLA (cm^2)	0.58 *	0.20 ns	0.77 **	-0.44 ns	-0.61 *	0.21 ns
LMA (g/m^2)	0.58 *	0.63 *	0.53 *	-0.22 ns	-0.38 ns	-0.22 ns
N_{mass} (%)	0.40 ns	-0.44 ns	0.01 ns	-0.01 ns	-0.10 ns	0.40 ns
N_{area} ($\mu g/cm^2$)	0.64 *	0.11 ns	0.32 ns	-0.24 ns	-0.54 *	0.33 ns
Photosynthetic characteristics						
$A_{max\text{-}area}$ ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$)	0.12 ns	-0.21 ns	0.16 ns	-0.22 ns	-0.01 ns	0.50 ns
$A_{max\text{-}mass}$ ($nmol\ CO_2\ g^{-1}\ s^{-1}$)	-0.12 ns	-0.40 ns	-0.07 ns	-0.10 ns	0.21 ns	0.49 ns
K (μmol photon $m^{-2}\ s^{-1}$)	0.36 ns	-0.22 ns	0.41 ns	0.16 ns	0.27 ns	0.55 *
Rs (μmol CO2 $m^{-2}\ s^{-1}$)	0.10 ns	-0.40 ns	0.43 ns	0.20 ns	-0.08 ns	0.18 ns
LCP (μmol photon $m^{-2}\ s^{-1}$)	0.30 ns	-0.34 ns	0.62 *	0.52 *	-0.05 ns	0.22 ns

Notes: $^{**}p < 0.01$; $^{*}p<0.05$; ns: not significant curves, one for each species in each site (Figure 3) and the mean photosynthesis rates at all light levels were well fitted with model curves.

Maximum photosynthesis rate on an area basis ($A_{max-area}$) was significantly greater on the Klaber (96,00) than the Klaber reference site for each species (Table 4). Scarlet oak had significantly greater $A_{max-area}$ than chestnut oak and red maple in both the Klaber (96, 00) and Klaber reference sites (Table 4). This is reflected by the greater N_{area} of scarlet oak because N_{area} was significantly correlated with $A_{max-area}$ (Table 5; Figure 4). $A_{max-mass}$ in the burned site was not significantly different from the reference site for each species (Table 4). Differences in $A_{max-mass}$ among species were significant only in the reference site where scarlet oak had significantly greater $A_{max-mass}$ than chestnut oak and red maple. Like maximum photosynthesis, K, Rs, and LCP were generally greater in the burned than in the reference sites and greater in oaks than in red maple (Table 4). This may indicate greater demand of light for seedlings in burned than in reference sites as well as by oaks compared to red maple seedlings.

Leaf water use efficiency

Although the oaks (particularly scarlet oak) generally had greater photosynthetic capacity than red maple, oaks also had greater stomatal conductance (g_{sw}) leading to lower instantaneous water use efficiency (WUE_i) compared to red maple (Figure 3). With increasing light level, g_{sw} increased linearly while photosynthesis rate (A) approached saturation and started to level off at high light. WUE of red maple and chestnut oak peaked at 200 μmol m^{-2} s^{-1} PAR in both sites while WUE of scarlet oak peaked at a higher light level because scarlet oak approached photosynthetic saturation at

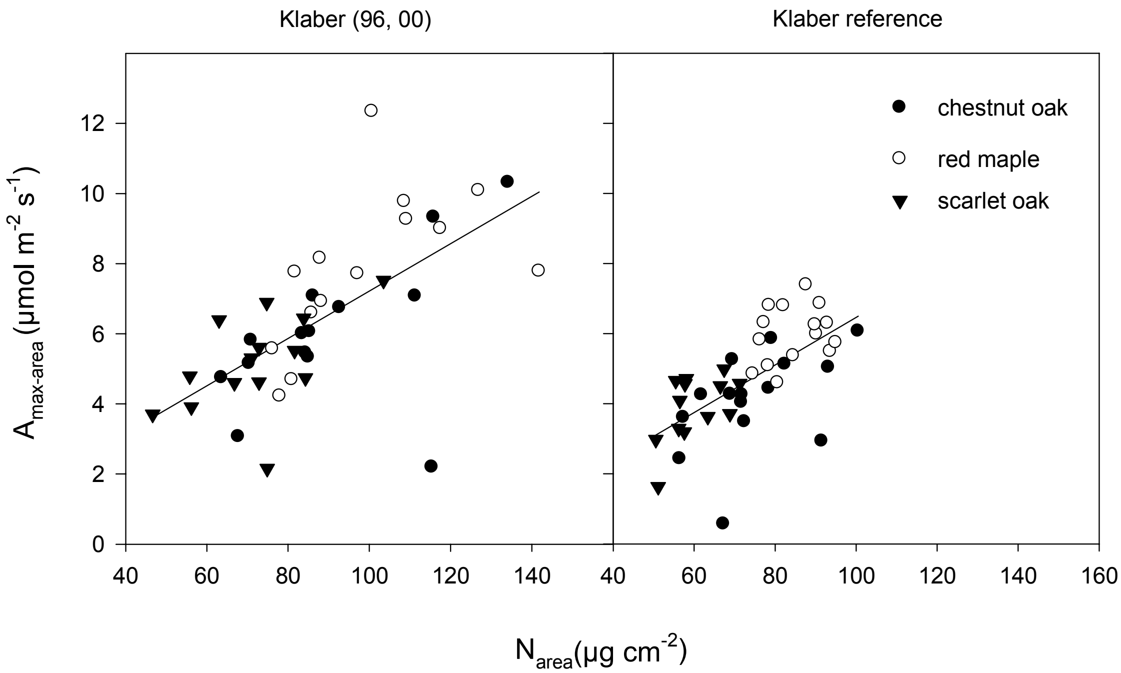


Klaber (96, 00)
Klaber reference
A (μmol m-2 S-1)
gsw (mol H2O m-2 s-1)
WUE (μmol CO2 mole H2O -1)
chestnut oak
scarlet oak
red maple
0
400
800
1200
1600

Figure 3

The responses of photosynthesis, stomatal conductance, and water use efficiency to light.

Photosynthetic light response curves, stomatal conductance (g_{sw}), and instantaneous water use efficiency (WUE_i) at difference irradiance levels for chestnut oak, scarlet oak, and red maple seedlings in the burned and reference sites. Each photosynthetic light response curve was fitted with Michaelis-Menten model. Parameters for each model were given in Table 4. WUE_i at different light levels were calculated by dividing photosynthetic rate (A) with g_{sw}. Asterisks (*) indicate significant species differences of means at the same light level.



Klaber (96, 00)
Klaber reference
chestnut oak
red maple
scarlet oak
$A_{max\text{-}area}$ (µmol m^{-2} s^{-1})
N_{area}(µg cm^{-2})
0
2
4
6
8
10
12
40
60
80
100
120
140
160

Figure 4

The correlations between leaf nitrogen content and maximum photosynthesis rate.

Relationships among nitrogen content per area (N_{area}) and maximum photosynthesis rate on area basis ($A_{max-area}$). Data were pooled for chestnut oak, scarlet oak, and red maple because relationships were not significantly different among species. Regression statistics were given in Table 6.

higher light. WUE of the three species were not significantly different at all light level in the reference site due to greater variabilities in g_{sw} (Figure 3).

Discussion

Prescribed fire, with its associated increase in understory light availability (measured as gap fraction; chapter 1), significantly increased height growth, total root mass, LMA, N_{area}, and TLA. I summarized the deviation of populations means at each burned site from its nearby reference site (Figure 5). Generally, with increasing number of burns, I found more significant differences between burned and nearby reference site for height growth, total root mass, and N_{area}. The patterns of t-values in LMA and gap fraction were similar because the two parameters were significantly correlated with each other. Compared to the oaks, red maple had either more or similar significant responses to prescribed fire for most measurements. Therefore, prescribed fire had a biologically significant effect on seedling growth and characteristics and the effects tended to be parallel among the three species or slightly greater for red maple. Thus, there is no evidence from this study of increased seedling performance of oak seedlings compared to red maple with prescribed burning.

What is the role of light in the interaction between fire and seedling responses? To answer this question, I examined the correlation between seedling aboveground growth and estimated belowground biomass with gap fraction for seedlings measured in 2001 and found significant relationships in the Klaber (96, 00) site (Table 5; Figure 1). Red maple exhibited greater response of aboveground growth (TLA and height growth) to gap fraction than the oaks; on the other hand, scarlet oak showed greater response of

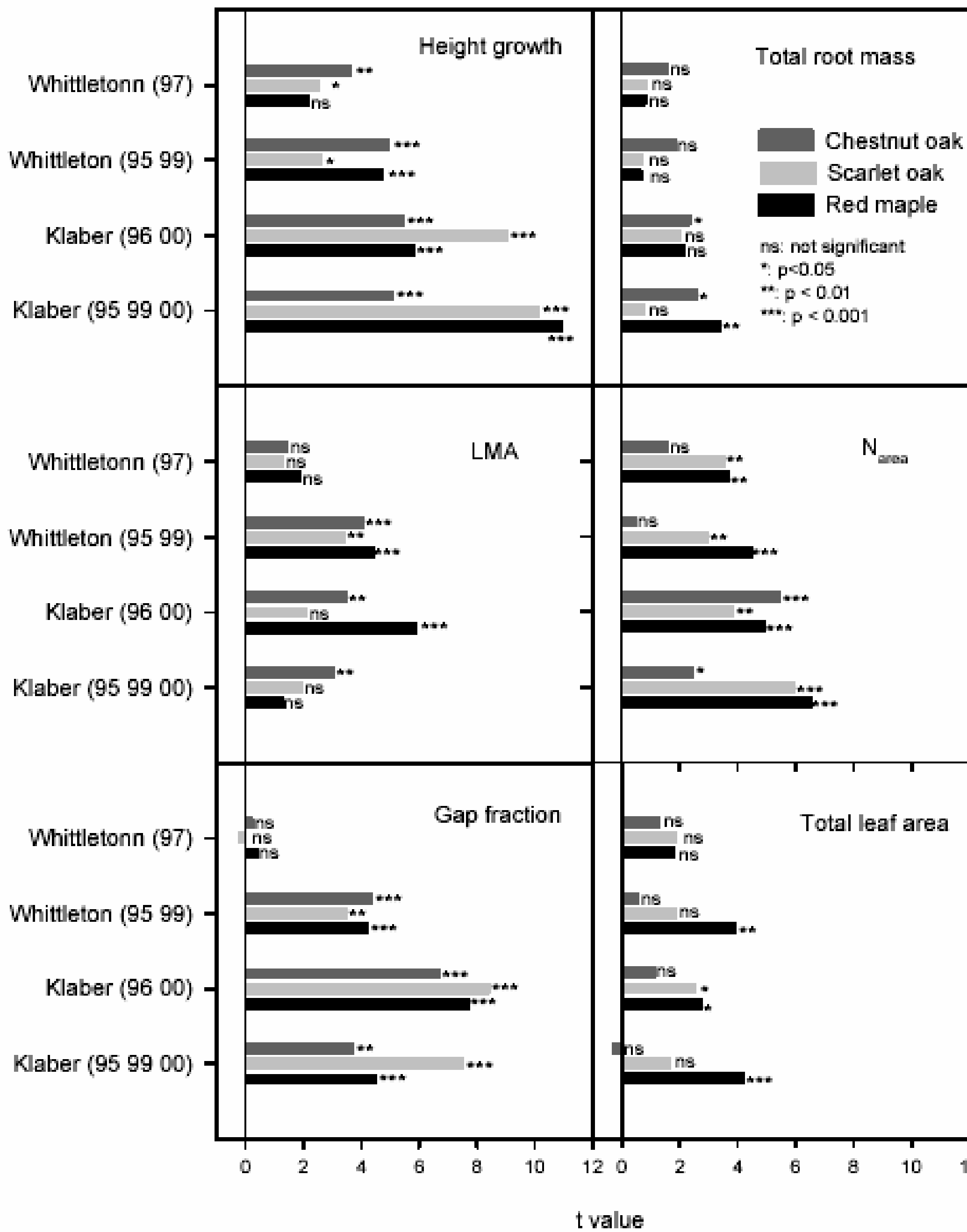

Height growth
Total root mass
LMA
N area
Gap fraction
Total leaf area
Whittletonn (97)
Whittleton (95 99)
Klaber (96 00)
Klaber (95 99 00)
Chestnut oak
Scarlet oak
Red maple
ns: not significant
*: p<0.05
**: p < 0.01
***: p < 0.001
t value

Figure 5

Responses of seedling characteristics to single and multiple fires.

Responses of seedling height growth, total root dry mass, leaf mass per area, leaf nitrogen content per area basis, gap fraction and total leaf area to single and multiple fires. The t values of two sample t tests between each burned site and its nearby reference sites were used to evaluate the responses.

root biomass to gap fraction than red maple (Table 5 and Figure 1). The same patterns of different biomass allocation between oaks and red maple were found using TLA as a predictor. This may indicate the potential of long-term repetitive burning on the control of red maple populations.

Gap fraction was also significantly correlated with seedling leaf characteristics, such as TLA and LMA in the Klaber (96 00) site (Table 6). LMA, which is a function of leaf thickness and density, is influenced by light environment (Young and Yavitt 1987, Abrams and Kubiske 1990, Kloeppel et al. 1993). The increase in LMA with increased mesophyll development in response to light is an important mechanism for increasing a plant's capacity to assimilate CO_2 (Oberbauer and Strain 1985, Jurik 1986, Oberbauer and Strain 1986, Ellsworth and Reich 1993, Kloeppel et al 1993, Le Roux et al. 1999). Although there was no direct relationship between gap fraction and most photosynthesis characteristics (Table 6), the increase in LMA of some seedlings (Figure 2A), clearly related to increasing gap fraction in the burned site (Figure 2B), resulted in the significantly greater mean N_{area} of all species in the Klaber (96, 00) site compared to the Klaber reference (Kull and Javis 1995). Because the majority of leaf nitrogen is used in the proteins of the Calvin-Benson cycle and thylakoids, N_{area} and $A_{max\text{-}area}$ are significantly correlated (Evans 1989, Figure 4). Thus, seedlings in the Klaber (96, 00) site acclimated to the increase in gap fraction by increasing LMA and N_{area}, which are associated with the increase of $A_{max\text{-}area}$ in the burned site. Again, there was no differential effect of prescribed fire among the three species and the associated change of light availability on the $A_{max\text{-}area}$ of the three species. All species exhibited greater $A_{max\text{-}area}$ in the Klaber (96, 00) site than the Klaber reference site (Table 4 and Figure 3).

The relationships between N_{area} and $A_{max\text{-}area}$ were not affected by either species or treatments (similar slopes and intercepts), which supports the notion of a universal relationship between leaf nitrogen content and maximum photosynthetic rate (Field and Mooney 1986, Chazdon and Field 1987). Therefore, N_{area} can be used as a surrogate measure of leaf maximum photosynthetic rate across species and sites. As N_{area} responded systematically to fire frequency for seedlings measured in 2000 (Figure 5), I presume $A_{max\text{-}area}$ also responded similarly to N_{area} and had greater $A_{max\text{-}area}$ with increasing number of burns.

Although I observed no interaction effect of prescribed fire and gap fraction on the leaf and photosynthetic characteristics of the three species, oaks tended to have greater values for photosynthetic parameters (Table 4) and the associated greater LMA and N_{area}, which may indicate the greater demand for light compared to red maple for the maintenance and perhaps construction of plant tissues. On the other hand, the moderate level of leaf N, LMA, and photosynthetic characteristics for red maple indicates its greater tolerance to low light conditions compared to the oaks, which may explain the ability of red maple to persist in conditions of relatively high shrub density and low light, and to outcompete oak species in these conditions. Therefore, although I did not observe any effect of prescribed fire and associated increase of gap fraction in improving oak seedling performance relative to red maple in the timeframe of this study, I believe the lack of light due to fire suppression would exacerbate the oak regeneration problem.

The ability of red maple to act as both an early and late successional species and flourish in diverse environmental conditions is believed to be the key attribute of its success in the eastern deciduous forest (Abrams 1998). In addition to the ability to survive in low light, red maple also exhibited significantly greater instantaneous water use efficiency (WUE_i, Figure 3). The greater WUE_i of red maple, perhaps through effective stomatal control (Kloeppel et al 1993, Abrams 1998), may be another important attribute for its survival on xeric ridgetop soils through dessication avoidance.

In response to disturbance such as prescribed fire, with its associated increase in light availability, red maple exhibited rapid aboveground growth (Table 5 and Figure 5; Abrams 1998). Therefore, prescribed fire can be used as a stimulus for the aboveground carbon investment of red maple. With long-term repetitive burning, the propagation of red maple seedlings may potentially be controlled by exhausting their belowgournd carbon reserves through repeated top-killings. Preliminary data from a long-term seedling population study suggests higher mortality of red maple than oak seedlings after multiple burns (Arthur unpublished data). Thus, any differential effect of prescribed fire on oaks versus red maple may become manifested only after long-term repetitive burning and result from greater belowground allocation of carbon reserves among oaks, compared to red maple.

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